SOCIAL AND ENVIRONMENTAL CONSTRAINTS ON BREEDING BY NEW ZEALAND SNIPE *Coenocorypha aucklandica*

A thesis submitted in fulfilment

of the requirements for the Degree

of

Doctor of Philosophy

by

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University of Canterbury

1989

...I confess that I could have lingered for weeks in the company of these fascinating birds, wondering over their loss of flight, large eggs and contracted range, watching the little creatures, brown like Autumn, harmless as Autumn's fallen leaves. There was something extra-ordinarily attractive in their trustfulness, an irresistable appeal in their absence of fear. We were back to the days of our first parents, to the golden dawn of the world, to that delectable garden where fear and pain and anger and sorrow were still unnamed, unknown. They were forms wholly lovable, wholly beautiful, living, moving and having their being in full view of us, to be adored like winter blossoms, to be touched as brides are touched. We could not but grieve that a few field naturalists on one long isle should be in sole enjoyment of what would have been a happiness to hundreds of pleasant people the world over.

Guthrie-Smith (1936: 188)

with 2 separate items
in pockets pages 106 and 144.

For Dorothy, Win and Carolyn,

for their love, support and encouragement

Contents

Abstract

New Zealand Snipe *Coenocorypha aucklandica* on the Snares Islands occurred at high densities and many males were unable to obtain territories. Territory ownership was a prerequisite for obtaining a mate, and most matings were monogamous. Territorial males guarded their mates, but did not exclude subordinate birds from territories. Females were courtship-fed by their mates for three weeks before laying; laying occurred earlier in years when food was more abundant, as females reached threshold laying weights sooner. Incubation was shared and took 22 days. Females that mated with males that were already paired incubated unaided; an egg in one such nest hatched after about 38 days.

The earliest hatch dates coincided with the annual peak in food availability. Broods were split at hatching, each parent caring for one chick independently. Chicks were fed by their parents for at least 41 days. Food availability during the period that chicks were reared was significantly higher than during the pre-chick period.

During chick-rearing, territories were usurped by subordinate males, which courted available females and sometimes bred. Failed pairs frequently renested, but no pairs were double-brooded. Some breeders of both sexes that lost their dependent chick bred a second time with a new mate while their first mate continued rearing the surviving chick.

Territory and mate fidelity of breeding adults were very high, and were not affected by breeding success in the previous year. Nonbreeding adults obtained a permanent territory and mate only if a territorial bird died. Prior residency was an important factor in acquiring a territory both within and between seasons. Mortality of adults during the nonbreeding season was density-dependent. However, exceptionally high mortality occurred in the winter following the 1982-83 El Niño event. Widespread reproductive failure and late breeding by snipe in 1982-83, and high mortality during the 1983 winter were probably caused by climate-induced reduction in their invertebrate food supply.

Compared with other snipe, New Zealand Snipe had much higher parental investment by both sexes, and much lower per pair potential reproductive output. The highly *K*-selected breeding system of New Zealand Snipe is considered an evolutionary response to high intraspecific competition for food during the breeding season. The low reproductive rate, and density-dependent mortality during the nonbreeding season indicate that New Zealand Snipe were limited by food throughout the year. These findings support Ricklefs' (1980) contention that bird populations in stable environments are limited by intraspecific regulatory processes.

Introduction

The ecology of landbirds on oceanic islands

The ecology of island landbirds has attracted the attention of biologists since Darwin (1859) used the Galápagos finches (Emberizidae: Geospizinae) to illustrate the principle of adaptive radiation through natural selection. Although the role played by the finches during the evolution of Darwin's ideas has probably been overstated (Sulloway 1982), island avifaunas have continued to play a seminal role in the development of ecological theory. Concepts that arose from studies of island faunas include species-area relationships (based on MacArthur & Wilson 1967), taxon cycles (e.g. Ricklefs & Cox 1972), density compensation (e.g. MacArthur *et al.* 1972, Wright 1980), adaptive radiation (e.g. Ford *et al.* 1973, Grant 1981), character release (e.g. Nilsson & Ebenman 1981, Boag & Grant 1984), and character displacement (e.g. Grant & Grant 1982, Schluter *et al.* 1985).

The reasons why ecologists have focussed on island ecosystems are many and varied (MacArthur & Wilson 1967, King 1985). Apart from their intrinsic appeal, islands are discrete ecosystems where populations and environmental changes can be monitored more readily than in mainland ecosystems. Island ecosystems often have a comparatively simple structure, allowing investigations of ecological principles and processes that may help us to understand more complex continental ecosystems. In addition, archipelagos may provide natural experiments where variation in size, isolation and ecology of different islands permits testing of evolutionary hypotheses (see MacArthur & Wilson 1967). However, perhaps the most compelling reason to study island birds is that many are endangered, and basic ecological information is required when formulating management policies.

About 93% of the bird species that have become extinct since AD 1600 lived on islands. Almost all these extinctions were the direct or indirect result of human activity (C. King 1984, W.B. King 1985, Moors 1985, Fuller 1987). Historically, the major causes of extinction have been habitat modification, and the deliberate or accidental introduction of predators and competitors. Avifaunas most affected by introduced predators were (and are) those on oceanic islands, e.g. the Mascarenes, the Seychelles, Hawaii and New Zealand (C. King 1984, Atkinson 1985, W.B. King 1985, Fuller 1987). The high proportion of endangered endemic bird species on oceanic islands (islands surrounded by deep water, never part of a continental landmass) compared with continental islands (islands that were connected to a continental landmass at Pleistocene times of low sea-level; see Williams 1981, Diamond 1984) has led to a dichotomy in ecological research on islands. Ecologists on continental islands (mainly in the northern hemisphere, the neotropics and around New Guinea) have focussed on ecological processes controlling community structure (e.g. Diamond 1969, Ebenman & Nilsson 1982, Stamps & Buechner 1985), while ecologists on oceanic islands (mainly in the southern hemisphere, Hawaii and the Indian Ocean) have focussed on conservation-based research (see reviews in Moors 1985).

Attempts to include oceanic island avifaunas within the framework of continental island models (e.g. Abbott & Grant 1976, Abbott 1978, Williams 1981, Diamond 1984) have not been successful, as intrinsic differences in the ecology of oceanic island landbirds have been overlooked. The models listed above are nearly all based on the premise that interspecific competition is the major factor governing the ecology and evolution of landbirds on islands (see Abbott 1980). This is clearly not the case for oceanic islands (Williams 1981, Diamond 1984).

Two important characteristics separate oceanic and continental islands. First, oceanic islands are more distant from potential sources of colonisation than continental islands. Isolation is recognised as the driving factor behind nonequilibrial avifaunas on oceanic islands (Abbott & Grant 1976, Williams 1981, Diamond 1984) as relatively few species are able to colonise new islands. A corollary of this is that interspecific competition will be less on oceanic islands, as fewer niches are occupied. Isolation was also (indirectly) a cause of the extremely high extinction rate of landbirds on oceanic islands in historic time. Predatory land mammals are not able to cross large stretches of ocean unaided; oceanic island birds evolved in the absence of carnivorous mammals, and were morphologically, behaviourally and ecologically unable to cope when mammals were introduced by humans (see King 1984, Moors 1985).

The second characteristic difference between continental and oceanic islands is that the climate of oceanic islands is moderated by the surrounding ocean, reducing seasonal variation in temperatures. Climatic moderation has had several subtle effects on oceanic island ecosystems (see Chapter 1). Year-round plant and invertebrate production has obviated the need for migration; very few landbirds that breed on oceanic islands are migratory, and this has undoubtedly contributed to the low rate of colonisation compared with continental landbirds.

Ricklefs (1980) demonstrated that clutch size in birds is directly related to seasonal variation in actual evapotranspiration; species in stable environments laid smaller clutches. Following Ashmole (1963), Ricklefs reasoned that population size during the breeding season was limited by density-dependent mortality during the nonbreeding season, and that the reproductive rate was determined by intraspecific competition for food during the breeding season. Landbirds on oceanic islands tend to be *K*-selected (e.g. Sagar 1985, McLean & Miskelly 1988), and their low rate of reproduction has compounded their vulnerability to increased predation.

As effective predators are absent from most unmodified oceanic islands, landbirds can occur at very high densities (e.g. Sagar 1985, Stamps & Buechner 1985, McLean & Miskelly 1988, Chapter 3). Since other factors that might regulate density (e.g. interspecific competition, predation) are relaxed or absent, intraspecific regulatory processes are probably more important for landbirds on oceanic islands than on continental islands.

Snipe breeding systems

I investigated the breeding ecology of New Zealand Snipe *Coenocorypha aucklandica* on the predator-free Snares Islands, to determine whether the population was limited by intraspecific competition for food. The main questions addressed were: (1) Did the breeding ecology of New Zealand Snipe show evidence that snipe were food limited? (2) How did variation in population density affect access to mates, and mortality rates? and (3) How was the timing of breeding related to food availability? The effects of annual variations in weather conditions on mortality and natality were also assessed. This is the first detailed field study of the ecology of *Coenocorypha* snipes.

Snipe belong to the family Scolopacidae, a diverse assemblage of about 87 extant species of shorebirds (Table 1). Most scolopacids are transequatorial migrants that breed in northern temperate to arctic latitudes. Only 13 species (9 snipe, 3 woodcock and 1 sandpiper) breed south of the equator.

Coenocorypha snipes are endemic to the New Zealand region (but see Balouet & Olson 1989); formerly they occurred throughout the three main islands of New Zealand, but local extinctions have confined them to four isolated island groups (Appendices 1 & 3). Extinctions on the New Zealand mainland occurred following Polynesian colonisation, and have

Table 1. Summary of breeding distribution, clutch size and migratory habits within the family Scolopacidae. Genera are separated by subfamily following Cramp & Simmons 1983. Breeding distribution is divided into three broad regions: Holarctic, Tropics and Southern. Separate entries are made for those genera (*Scolopax* and *Gallinago*) that have members breeding in more than one region. Most tropical species breed in the southern hemisphere, and are included as southern species in the text. Data from Maclean 1972, Johnsgard 1981, Cramp & Simmons 1983, Hayman *et al*. 1986, and Sæther *et al*. 1986.

Genus	Common name	Number of species	Breeding distribution	Clutch size	Migratory?
Limosa	godwits	4	Holarctic	4	Yes
Numenius	curlews & whimbrels	8	Holarctic	4	Yes
Bartramia	Upland Sandpiper	1	Holarctic	4	Yes
Tringa	'shanks' & sandpipers	10	Holarctic	4	Yes
Catoptrophorus	Willet	1	Holarctic	4	Yes
Xenus	Terek Sandpiper	1	Holarctic	4	Yes
Actitis	sandpipers	2	Holarctic	4	Yes
Heteroscelus	tattlers	2	Holarctic	4	Yes
Prosobonia	Tuamotu Sandpiper	1	Tropics	2	No
Arenaria	turnstones	2	Holarctic	4	Yes
Phalaropus	phalaropes	3	Holarctic	4	Yes
Scolopax	woodcock	3	Holarctic	4	2 spp.
		3	Tropics	2	No
Coenocorypha	New Zealand snipe	2	Southern	2	No
Gallinago	snipe	7	Holarctic	4	Yes
		6	Tropics	2-3	No
		2	Southern	2	No
Lymnocryptes	Jack Snipe	1	Holarctic	4	Yes
Limnodromus	dowitchers	3	Holarctic	2-4	Yes
Aphriza	Surfbird	1	Holarctic	4	Yes
Calidris	arctic sandpipers	19	Holarctic	4	Yes
Eurynorhynchus	Spoon-billed Sandpiper	1	Holarctic	4	Yes
Limicola	Broad-billed Sandpiper	1	Holarctic	4	Yes
Micropalama	Stilt Sandpiper	1	Holarctic	4	Yes
Tryngites	Buff-breasted Sandpiper	1	Holarctic	4	Yes
Philomachus	Ruff	1	Holarctic	4	Yes

been attributed to introduced kiore *Rattus exulans* (Holdaway 1989). Extinctions of the Little Barrier Snipe *C.a. barrierensis* (c.1870) and Stewart Island Snipe *C.a. iredalei* (1920 - 1964) coincided with introductions of cats *Felis catus* to Little Barrier Island, and cats, Weka *Gallirallus australis* and ship rats *Rattus rattus* to several islands off Stewart Island (Appendices 1 & 3). Clearly, these snipe are extremely vulnerable to introduced predators, although there is no direct evidence of eggs, chicks or adults being taken.

Although *Coenocorypha* snipes are numerous on most islands where they occur (Fleming 1939 & 1948, Warham 1967, Bell *in* Edgar 1972, Warham & Bell 1979) they have attracted little attention due to the infrequent (and often short) visits made to the islands, the thick ground cover, their cryptic plumage colouration and 'skulking habit' (Stead 1948, Warham & Bell 1979). Published information on the breeding biology of *Coenocorypha* snipes is anecdotal. No nests of Auckland Island Snipe *C.a. aucklandica* or Antipodes Island Snipe *C.a. meinertzhagenae* have been described, but Oliver (1955) described an egg and nestling of Auckland Island Snipe, and there is an egg and chick of Antipodes Island Snipe in the British Museum (Natural History)(Warham & Bell 1979). Forbes (1893) described the eggs and chick of Chatham Island Snipe and gave the clutch size as three. A nest found more recently contained two eggs (Tennyson *in* Gaze 1986). Eggs were found from September to December by Munn (*in* Booth 1983).

The extinct Stewart Island Snipe was studied on Big South Cape Island in November 1923 by Guthrie-Smith (1936), and in December 1931 by Stead and Wilson (Wilson 1959). Both parties found at least two and three nests respectively, all with two eggs. Guthrie-Smith described nests and eggs, and observed that both sexes incubated, and that each pair cared for a single chick. Photographs of snipe nests and eggs were published by Guthrie-Smith (1936) and Wilson (1959).

Four nests of Snares Island Snipe *C.a. huegeli* were found in December 1947 (Stead 1948). Stead described eggs and nests, and gave the laying interval of the two eggs as two days. Anderson (1968) studied Snares Island Snipe during January and February 1967. He did not find any nests, but captured six chicks a total of 10 times. Anderson never saw more than one chick with an adult, and suggested that each parent accompanied one of the chicks. He also reported that parents fed chicks until they were well-feathered, although chicks also foraged for themselves. Horning & Horning (1974) reported a newly-hatched chick on 4 May 1972. Sagar (*in* Edgar 1977) found three nests of Snares Island Snipe, each with two eggs, in November and December 1976.

Information on the breeding systems of most other snipes is even more scant. Of the 15 species in the genus *Gallinago*, clutch sizes are known for 14, but sample sizes for all seven southern hemisphere species are probably less than five (see Maclean 1972, Tuck 1972, Johnsgard 1981, Sæther *et al.* 1986). The breeding system of Common Snipe *G. gallinago* is well known (see Table 1.1): matings are monogamous, the clutch of four eggs is incubated by the female, and both parents assist with brood rearing. A similar system has been claimed for Swinhoe's Snipe *G. megala*, Pintail Snipe *G. stenura* and Japanese Snipe *G. hardwickii*, but accounts are contradictory (see Tuck 1972, Johnsgard 1981). The Great Snipe *G. media* is a lek-breeder (Lemnell 1978, Avery & Sherwood 1982, Höglund & Lundberg 1987) in which the female incubates unaided (Løfaldli 1985). Claims that the male Great Snipe assists with brood-rearing (Niethammer *in* Tuck 1972) seem doubtful as males do not assist with brood care in any other lek-breeding bird. Mating and parental care systems are not known for the other 10 *Gallinago* snipes.

Other members of the family Scolopacidae have been studied in greater detail (see reviews in Pitelka *et al.* 1974, Johnsgard 1981, Oring & Lank 1984, Walters 1984). Almost all are migratory shorebirds that breed in the holarctic and winter in the tropics or southern hemisphere (Hayman *et al.* 1986 and Table 1). Mating systems are extraordinarily variable, and include monogamy, double clutching, serial polygamy, sequential polygyny, sequential polyandry, simultaneous polygyny, simultaneous polyandry, and lek-breeding (some species use more than one strategy, depending on the availability of mates; Emlen & Oring 1977, Oring 1982). Parental care is shared in most species, but is performed entirely by one or other sex in several species (see references above). However, all but two of the scolopacid species breeding in the holarctic lay clutches of four eggs (see Table 1 and Chapter 1). The primitive breeding system is presumed to be monogamy, with shared incubation of the four-egg clutch, and shared brood care (Jenni 1974, Pitelka *et al.* 1974).

No published study describes in detail the breeding system of any of the 13 scolopacid species that breed in the southern hemisphere.

Thesis format

This thesis is a collection of nine papers, each written in the style of the journal *Ibis*. Five papers form the main body of the thesis, and four are given as appendices. Each paper is complete in itself, although a single reference list is given before Appendix 1. This format has, inevitably, led to some repetition in the 'Study area and methods' section of each paper. Appendices 1 and 3 are reprints of published papers, and so have separate acknowledgements and reference lists.

In the first paper (Chapter 1), I describe the breeding systems of New Zealand Snipe and Chatham Island Snipe, focussing on features of their breeding ecology that could be affected by food availability.

Comparisons are made with the breeding system of Common Snipe, the only other snipe species that has been studied in detail (see above). Further details of *Coenocorypha* breeding ecology are given in Appendix 2, where I describe breeding seasons, nests, eggs, incubation patterns, and chick development for Snares Island Snipe and Chatham Island Snipe. Chapter 1 and Appendix 2 provide background information for the remaining four chapters.

In Chapter 2, I describe incubation patterns associated with polygyny in New Zealand Snipe. Most snipe were monogamous, with shared incubation and biparental care of the chicks. However, two males were polygynous, and did not assist at supernumerary nests. This system appeared analogous to resource defense polygyny in passerines (e.g. Orians 1961, 1969, Verner 1964, Verner & Willson 1966) but was considered unusual for a species with (apparently) obligate biparental care.

The social structure and population dynamics of New Zealand Snipe are described in Chapter 3. Dispersal of breeders and juveniles is discussed in terms of mating opportunities. The high degree of natal philopatry, mate fidelity and territory fidelity were considered consequences of the non-migratory nature of the population, and the high population density. Mortality in the nonbreeding season was found to be density dependent, except for during the winter after the severe 1982-83 El Niño event. The effects of El Niño are further discussed in Chapter 4. These two chapters demonstrate that while high density snipe populations may be regulated by density-dependent processes, stochastic events can drastically alter natality and mortality rates.

In Chapter 5, I investigate the relationship between food availability and breeding by snipe. If snipe are limited by food, then variation in food availability should influence the timing and success of breeding. Samples of soil invertebrates collected before and during two snipe breeding seasons were used to demonstrate the stability of the food resource for snipe within and between seasons. The effect of environmental stability on breeding is discussed.

Appendices 1, 3 and 4 provide information on the distribution, history, conservation, mythology and behaviour of *Coenocorypha* snipes. Appendix 5 gives an analysis of the diet of snipe on the Snares Islands, based on faecal remains (from Miskelly 1984).

Chapter 1

Breeding systems of New Zealand and Chatham Island Snipes; are they food limited?

Ibis (accepted manuscript).

Abstract

New Zealand Snipe *Coenocorypha aucklandica* were studied over six breeding seasons on the Snares Islands. The study area (7.5 ha) held about 20 pairs at a density of 3.2 ± 0.5 pairs/ha, plus 5 to 25 nonterritorial birds. Most matings were monogamous, but simultaneous polygyny was recorded in one territory (by two different males) in four consecutive seasons. Males courtship fed females before egg-laying. The typical clutch was two eggs, laid three days apart. Incubation was shared equally by the sexes in monogamous pairs and took 22 days. Some females with polygynous mates attempted to incubate unaided, which took about 38 days. Broods were split at hatching, with the male caring for the first chick to leave the nest. Chicks were fed by adults for at least 41 days, and did not become independent until about 65 days old. Growth rates were slow compared to Common Snipe *Gallinago gallinago* and full plumage took about 54 days to attain. No pairs were double-brooded, but 43% of pairs that failed during incubation or early chick-rearing renested together. Some breeders of both sexes who had lost their dependent chick bred a second time with a new mate while their first mate continued rearing the surviving chick (sequential polygyny and polyandry). Hatching success was 80%, and fledging success was 48%. Each pair produced, on average, 0.6 fledglings per year, and about a third of these were controlled at age one year (0.2 per pair).

Chatham Island Snipe *C. pusilla* were studied on Rangatira Island during the 1983-84 breeding season. Breeding density was about 5.6 pairs/ha. The breeding system was very similar to that for *C. aucklandica*, but chicks became independent at about 41 days old. Hatching success was 89%.

Compared to Common Snipe, *Coenocorypha* snipes occurred at high densities, had courtship feeding, large eggs, a long egg interval, a small clutch, shared incubation and a long incubation period. Nest desertion rates were high, but overall hatching success was also high, chick growth rates were slow, there was a long period of chick dependence

and a long relaying interval following nest failure or chick loss. Survival rates of both adults and chicks were high. These differences are attributed to the absence of predation, and to intense intraspecific competition for food in a stable environment.

Introduction

Most shorebirds in the family Scolopacidae typically lay clutches of four eggs. Of the 72 species breeding in the holarctic, only two dowitcher species *Limnodromus* spp. usually lay smaller clutches (Maclean 1972, Walters 1984, Sæther *et al.* 1986). In contrast, at least ten of the 13 species breeding in the southern hemisphere lay modal clutches of between one and three eggs (clutch sizes of three species unknown; Maclean 1972, Walters 1984); nine of the scolopacid species that breed in the southern hemisphere are snipe (Hayman *et al.* 1986). Breeding systems of scolopacids that lay small clutches are poorly known (Maclean 1972, Jehl & Murray 1986, Sæther *et al.* 1986). Furthermore, it is not clear why reduced clutches are a feature of shorebirds breeding in the southern hemisphere (Maclean 1972, Winkler & Walters 1983, Walters 1984).

The snipe genus *Coenocorypha* comprises two extant species found on outlying islands of New Zealand (Appendix 1). New Zealand Snipe *C. aucklandica* and Chatham Island Snipe *C. pusilla* are non-migratory and are considered the most morphologically primitive snipes (Lowe 1915, Strauch 1978). As *Coenocorypha* snipes occur at high densities in environments free of effective predators or foraging competitors (McLean & Miskelly 1988, Chapter 3), populations may be limited by intraspecific competition for food. In this study I investigate parameters of the breeding systems of New Zealand and Chatham Island Snipes that could potentially be constrained by food availability. Their breeding systems are compared with that for Common Snipe *Gallinago gallinago*, the only other snipe species that has been studied in sufficient detail. An hypothesis for the reduced clutch size and other *K*-selected traits of *Coenocorypha* snipes is outlined.

Study areas and methods

Snares Islands

New Zealand Snipe (race *huegeli*; Fig. 1.1) were studied on Main Island, Snares Islands Nature Reserve (48°02′S 166°36′E) in the New Zealand

Figure 1.1. Adult female New Zealand Snipe, Snares Islands.

subantarctic during seven expeditions between December 1982 and December 1987. Observations spanned the months September to March (total 477 days and 134 nights in the field), and included parts of six breeding seasons.

A 7.5 ha study area of *Olearia lyalli* forest north of the Biological Station (Warham 1967) containing about 20 snipe territories was marked out in a 20 m grid. Snipe of all ages were captured with a handnet during the day, or with a spot-light and handnet at night. All adult snipe (n = 93) resident in the study area were individually colour-banded for the duration of the study, and 73 chicks were given numbered metal bands or year colour-codes. Adult snipe were sexed by measurements and by sex-specific displays recorded after marking (unpubl. data). Pairs were identified by prolonged consorting, courtship feeding, mating, or attendance at the same nest, as observed during daily surveys of the study area.

All breeding attempts in 1985-86 and 1986-87 were detected by observing behaviour of adults and by regular monitoring of female body-weight, cloacal swelling and brood patch condition. Forty-five nests were located by tracing the source of calls (n = 20), systematic searching (n = 19), chance disturbance of incubating adults (n = 4), or following returning adults (n = 2). The 14 nests that were not found in 1985-86 and 1986-87 (11 successful, 3 unsuccessful) were included in overall analyses of breeding success, but not in the analysis of hatching success. Eighty-one eggs were measured to 0.1 mm and weighed to 0.5 g when found. Forty eggs were weighed subsequently to determine rates of water loss during incubation. Fresh egg-weights were measured directly (n = 9) or estimated by adding estimated water loss (0.18 g/day) to the weight when found (n = 68). Weights for four eggs at two nests where incubation was not shared were estimated from linear measurements (Chapter 2), as water loss was less at nests with lower incubation constancy. Nests were checked daily, or more frequently during laying and hatching. Hides were erected at four nests (three with shared incubation and one with solo incubation). Five 24-h observations of incubation constancy (percent of time a bird was on the nest) were undertaken in the middle of the incubation period. A chart recorder, light beams and photo-electric cells were installed at two nests in addition to those above, and gave two 24-h tracings of incubation constancy.

Chicks were banded in the nest or when first captured. Developmental data were obtained from 35 known-age chicks between hatching and age 78 days. As dependent young were always present when I left the island (February or March), fledging success and survival to independence could only be calculated for chicks that hatched out at least 30 and 65 days respectively before my departure. However, survival from hatching to age one-year-old did not differ for chicks aged more or less than 30 days at my departure (X^2 = 0.004, n.s.). Breeding success was only determined in detail for 1985-86 and 1986-87, when observations spanned four months and covered the entire laying season (but see Chapter 4).

Chatham Islands

Chatham Island Snipe (Fig. 1.2) were studied on Rangatira (South East) Island Nature Reserve (44°21'S 176°10'W), Chatham Islands, from 25 November 1983 to 18 January 1984 and 7 to 15 July 1986 (61 days, 20 nights). The main study area was 4.3 ha of *Olearia traversi* and *Plagianthus regius* forest around the field hut, and contained about 24 snipe territories. Methods of capture and observation were similar to those for New Zealand Snipe.

Thirty-five adults were individually colour-banded, and 47 chicks were given numbered metal bands. Fourteen nests were found by systematic searching, and 28 eggs were measured. Fresh egg weights were estimated from linear measurements using the equation from Chapter 2.

Developmental data were obtained from 28 known-age chicks between hatching and age 89 days.

Measurements are given as mean ± s.d., with range in parentheses, unless otherwise stated.

Figure 1.2. Adult male Chatham Island Snipe, Rangatira Island.

Results

Breeding density

The density of New Zealand Snipe in the study area over six breeding seasons was 3.2 ± 0.5 territorial pairs/ha (2.6 - 3.8 pairs/ha). Total density (including nonterritorial birds) was 8.2 ± 2.2 birds/ha (range over six years 5.4 - 11.5 birds/ha). Some nonterritorial birds attempted to breed during chick-rearing of territorial pairs (Chapter 3).

The density of Chatham Island Snipe in the study area on Rangatira Island was about 5.6 pairs/ha, but I was not able to confirm the presence of nonterritorial birds due to my late arrival on the island.

Mating system

Of 83 territory-holding male New Zealand Snipe from six breeding seasons, 79 (95.2%) had a single mate at the start of the breeding season. In each of four breeding seasons, one male had two or three mates simultaneously (see Chapter 2). Two different males on the same territory were involved; both held the territory for two consecutive years each. This territory was on a peninsula and had only a small defended boundary at its base, allowing the territory holders to defend a large area of high quality habitat. Both males had been monogamous for at least two breeding seasons before being polygynous. These simultaneously polygynous males assisted in incubation at one nest only, leaving the supernumerary females to incubate by themselves (Chapter 2).

The other 19 territories occupied each season had 3 - 7 adjoining territories, and all held monogamous pairs. Although 2 - 7 unpaired females were present in these 19 territories between 1985 and 1987, none attempted to breed with a male that was already paired. Two males were observed to court additional females around the date that their mates were laying; neither attempt at polygyny was successful, and the males shared incubation at their first mates' nests.

Some breeders of both sexes which had lost their dependent chick paired with new mates and attempted to breed again while their original mate continued to rear the surviving chick from the first brood (sequential polygyny and polyandry; see Renesting).

Incubation was shared at all ten nests of Chatham Island Snipe for which incubation patterns were determined, suggesting that all females observed were in monogamous relationships (though it is possible that the males had other mates).

Courtship and copulation

New Zealand Snipe pairs consorted for up to 108 days before laying, but it is not known if pairs stayed together during autumn and winter.

Courtship feeding was observed for eight different pairs on eight days (total number of food passes = 41, 1 - 22 per bout). All food passes were from male to female. Courtship feeding occurred from 62 days before the first egg of the pair was laid to the day before the second (final) egg was laid. Excluding the one outlier, courtship feeding was seen only in the three weeks before laying. Copulation was observed on ten days, ranging from 62 to four days before the first egg of the pair was laid. Ignoring the one outlier (a different pair to the record of early courtship feeding), copulation occurred 14.4 ± 6.3 days (4 - 21 days, n = 9) before the first egg was laid. Courtship feeding was not required to solicit copulation; only one pair was seen to courtship feed and copulate on the same day, but in this case courtship feeding immediately preceeded copulation.

No pairs of Chatham Island Snipe were seen together during nine days on Rangatira Island in July 1986 (austral winter). Courtship feeding was observed on two days in 1983-84: on 28 November a male fed his mate nine times immediately after they had mated (the only copulation seen for Chatham Island Snipe); on 4 December a pair with recently independent young was seen courtship feeding (this pair was not observed to breed again during the ensuing 45 days).

Laying

Egg intervals were determined within 16 hrs for five nests of New Zealand Snipe. The mean egg interval was 72 h 24 min (range 67 h 40 min ± 3 h 15 min to 76 h 23 min ± 1 h 13 min). The shortest and longest egg intervals (also the most accurate) were for the same female in consecutive breeding seasons.

No information on laying was obtained for Chatham Island Snipe.

Eggs

Of the 42 New Zealand Snipe nests with complete clutches found during this study, 41 had two eggs and one had three eggs. Fourteen snipe nests with complete clutches have been found by previous workers on the Snares Is; all had two eggs (Stead 1948, B.R. Keeley *in litt.*, P.M. Sagar *in litt.*, P.E.N. Wright *in litt.*). Thus, of 56 complete clutches, 55 (98.2%) had two eggs and one (1.8%) had three eggs.

Fresh weight for nine New Zealand Snipe eggs was 24.0 ± 1.0 g (22.3 - 25.5 g). Estimated fresh weight for all 81 eggs was 23.7 ± 1.1 g (21.1 - 26.7 g). Thus, each egg was about 20.4% of the mean adult female body-weight (i.e. 116.0 g, n = 62).

Between 1971 and 1985 at least 51 nests of Chatham Island Snipe were found on Rangatira and Mangere Islands; 49 nests (96.1%) contained two eggs (pers. obs., Gaze 1986, M.D. Dennison *in litt.*, C.H. Hay *in litt.*, D.V. Merton *in litt.*, R.B. Morris pers. comm.). Forbes (1893) reported the clutch size of Chatham Island Snipe to be three eggs, but did not state the number of nests on which this was based; his figure has been repeated often (eg. Oliver 1955, Maclean 1972, Falla *et al*. 1979). A three-egg nest was found on Rangatira Island on 27 December 1971 (L.B. McPherson pers. comm.) and a pair with three recently hatched chicks was seen c.5 December 1979 (H.A. Robertson *in litt*.). A four-egg nest on Mangere Island on 15 October 1976 (R.B. Morris pers. comm.) was possibly laid by two females.

Eggs of Chatham Island Snipe were about 32% smaller than those of New Zealand Snipe. Mean estimated fresh egg-weight was 16.1 g, i.e. about 18.9% of the mean adult female weight of 85.4 g (n = 24).

Incubation

Incubation began when the second egg was laid (observed at five nests). Incubation was shared equally by the sexes at 95% of nests (Appendix 2), but was undertaken solely by the female at two nests (where the male was simultaneously polygynous; see Mating system, and Chapter 2). Incubation constancy was 100% at five nests with shared incubation, but was 60 - 83% at the two nests with female single-sex incubation (Chapter 2).

Incubation period (from laying of the last egg to hatching of either egg) was determined within eight hours for three nests with shared incubation. The mean incubation period was 22 d 2 h (range 21 d 11 h ± 8 h to 22 d 13 h ± 6 h). One female incubating by herself successfully hatched an egg after 37 - 39 days of incubation (Chapter 2).

Incubation period was not determined for Chatham Island Snipe.

Care of young

Broods were always split as soon as the young left the nest; the two chicks were never seen together, and no adult was seen with more than one chick (n = 26 two-chick broods for New Zealand Snipe; n = 7 two-chick broods for Chatham Island Snipe). The male cared for the first chick to leave the nest in both New Zealand (n = 10) and Chatham Island (n = 5) Snipes. An adult that lost its chick (or never had one) did not assist its mate to rear the other chick.

New Zealand Snipe chicks were not seen probing for themselves during the first 12 days. After this, they continued to be fed partly by their parents until at least 41 days old, and consorted with their parents for a further 2 - 5 weeks. The youngest independent chick seen was 57 days old, but another chick was still with its parent at 78 days old. The minimum estimate for age of independence for 15 chicks was 65 ± 6 days (57 - 79 days).

The energetic cost of chick-rearing by New Zealand Snipe was estimated by comparing body-weights of successful versus failed breeders during the 65 days after hatching (or nesting failure). Body-weight did not vary with time for any of the four groups considered (successful females r_{19} = -0.19, failed females r_{15} = -0.27, successful males r_{27} = -0.36, failed males r_8 = 0.05; all $P > 0.05$). Successful female breeders weighed 111.4 ± 5.8 g (103.0 - 120.0 g, n = 21), significantly less than failed female breeders (119.3 ± 6.8 g, range 109.3 - 133.0 g, n = 17; Mann-Whitney U test P = 0.001). The difference in weight between successful and failed male breeders was not significant, but showed the same trend; successful male breeders weighed 100.8 ± 4.6 g (92.5 - 112.0 g, n = 29), failed male breeders weighed 103.8 ± 5.0 g (95.0 - 110.0 g, n = 10; Mann-Whitney U test P = 0.08). There was no significant difference between weights of successful and failed breeders of both sexes before hatching or nesting failure occurred. The lower body-weights of successful breeders indicates that there was an energetic cost to chick-rearing.

Although I never saw more than one Chatham Island Snipe chick with an adult, H.A. Robertson (*in litt.*) recorded a pair with three recently hatched chicks (see Eggs).

The youngest Chatham Island Snipe chick seen to feed itself (probing) was 18 days old. Chicks continued to be fed by their parents until at least 29 days old, and consorted with their parents for a further 1 - 3 weeks. The youngest independent chick seen was 33 days old, and the oldest accompanied chick was 46 days old. The minimum estimate for age of independence for 12 chicks was 41 ± 5 days (33 - 47 days).

Development of young

The mean weight of 28 New Zealand Snipe chicks just after hatching was 15.5 ± 0.9 g (14.0 - 18.0 g), which was about 65.4% of fresh egg-weight, and 14.3% of mean adult weight. Plumage development and down loss took about 54 days, and flight was first recorded at 30 days (Appendix 2).

Recently hatched Chatham Island Snipe chicks weighed 11.0 ± 0.7 g (10.0 - 12.0 g, n = 12), which was about 68.3% of fresh egg-weight, and 13.9% of mean adult weight. Plumage development and down loss took about 47 days, and flight was first recorded at about 21 days (Appendix 2).

New Zealand and Chatham Island Snipe chicks grew much more slowly in relation to their weight asymptotes than Common Snipe chicks (Fig. 1.3). Growth constants (K_G) for the three species are given in Table 1.1.

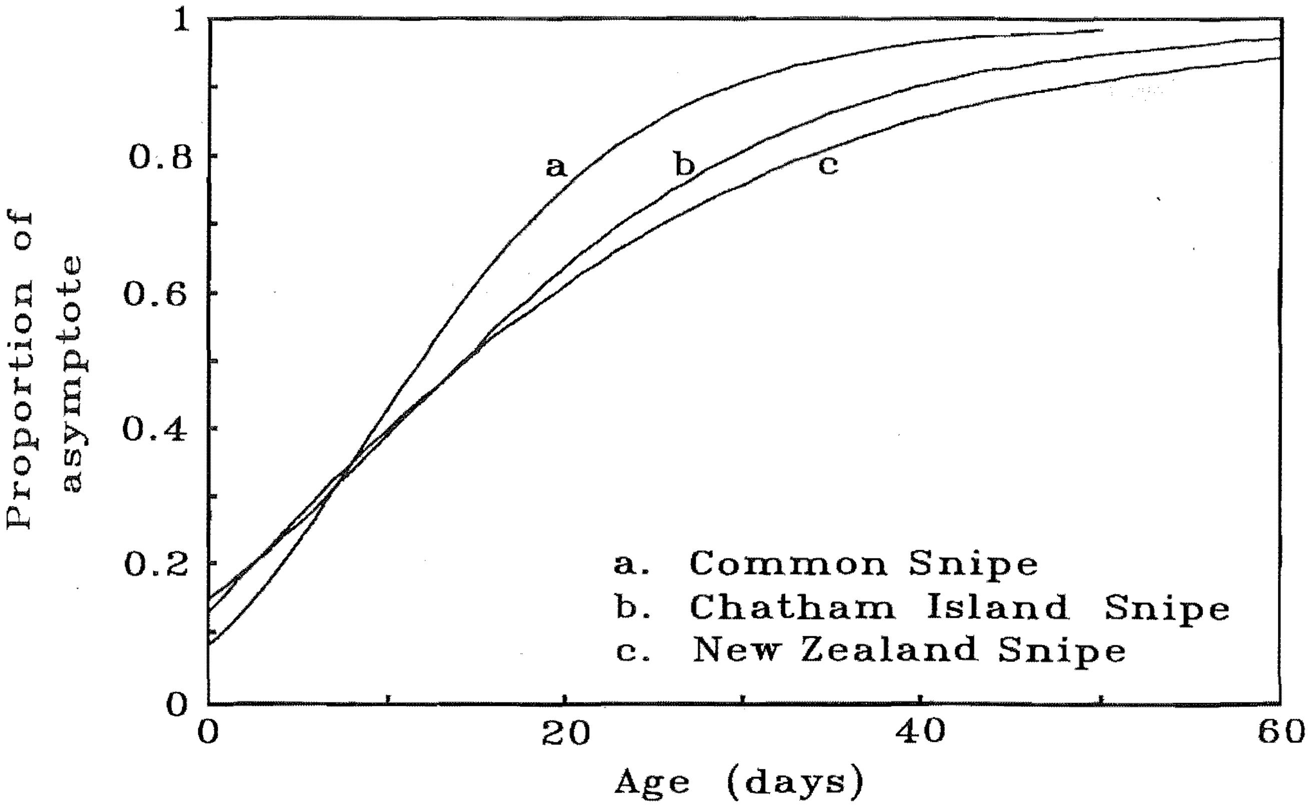

Figure 1.3. Weight growth rates of three species of snipe as a proportion of their growth asymptotes. Common Snipe (*Gallinago*) chicks were about 25% smaller in relation to adult body-weight at hatching compared with Chatham Island Snipe and New Zealand Snipe (*Coenocorypha* spp.). However, Common Snipe chicks grew much faster, reaching 95% of the asymptote after only 35.4 days (cf. 48.7 days for Chatham Island Snipe and 59.6 days for New Zealand Snipe). Gompertz growth equations obtained from Green (1985a; Common Snipe) and Appendix 2 (Chatham Island Snipe and New Zealand Snipe).

Renesting

Of 14 New Zealand Snipe pairs whose breeding attempts failed during incubation or when the chicks were less than five days old, six (43%) renested together. Pairs that failed after 8 January did not renest (n = 5). If a bird of either sex lost its chick (or one of the eggs had not hatched) while its original mate was still caring for a chick, it would attempt to obtain a new mate. Of seven emancipated males whose mates still had chicks, three obtained new mates and one of these pairs laid (sequential polygyny). Of 12 emancipated females whose mates still had chicks, six obtained new mates and three laid a second clutch (sequential polyandry).

Table 1.1. Comparison of the breeding systems of New Zealand Snipe, Chatham Island Snipe and Common Snipe. Data on incubation for New Zealand Snipe do not include the two nests with female single-sex incubation (see Chapter 2). Data for Common Snipe from Tuck 1972, Cramp & Simmons 1983, Green 1985a, 1985b & 1988, Sæther *et al*. 1986, Green *et al*. submitted MS.

	New Zealand Snipe	Chatham Island Snipe	Common Snipe
Breeding density (prs/ha)	3.2	5.6	0.4
Mating system	95% monogamy	monogamy	monogamy
Courtship feeding	yes	yes	no
Egg interval (days)	3	-	1
Clutch size	2	2	4
Egg size as % of ♀ weight	20.4	18.9	16.5
Incubation	shared	shared	female only
Incubation constancy (%)	100	100	78.2
Incubation length (days)	22	-	18 - 20
Hatching success by nest (%)	80	89	36
Brood splitting	male takes first chick	male takes first chick	male takes first 2 chicks
Neonate weight as % of adult weight	14.3	13.9	10.6
Weight growth constant ($\underline{K}_G$)	0.070	0.074	0.111
Fledging (days)	30	21	20
Independence (days)	c.65	c.41	c.21

Seven females relaid 36 ± 13 days (19 - 53 days) after failure of their first breeding attempt. The length of the relaying interval was not correlated with the date or year of failure. No female laid more than two clutches in a season, but two polygynous males sired three and four clutches respectively in a season. None of the pairs was double-brooded, but one male commenced incubating at a nest with a different female after raising his first chick for eight weeks (see Chapter 2). Of the three sequentially polyandrous females that laid a clutch with their second mate, only one female successfully hatched an egg from the second clutch. This female raised one chick from the second clutch, and her first mate raised one chick from the first clutch.

One female Chatham Island Snipe laid a second clutch about nine days after the artificial termination of her first breeding attempt.

Breeding success

Of 62 pair-years of New Zealand Snipe in the study area over four breeding seasons, 42 pairs (68%) attempted to breed. Of 40 nests studied, 26 (65%) hatched both eggs, 32 (80%) hatched at least one egg, and eight (20%) failed totally. Of the eight nests that failed, seven were deserted and one (the only three-egg nest found) was destroyed by a Sooty Shearwater *Puffinus griseus* attempting to scratch out a nest burrow.

Of the 79 eggs laid in these 40 nests, 58 (73.4%) hatched (a mean of 1.45 eggs per nest, and 1.81 eggs per successful nest). Six eggs that were incubated full term failed to hatch; one was infertile, three were slightly cracked and addled (cause of damage unknown) and two chicks died at hatching.

Some chicks came from nests that were not found, or were still dependent when I left the Snares Islands, hence sample sizes differ for each age class in the following summary.

Twelve out of 25 (48%) chicks banded in the nest survived to fledging (age 30 days) and ten fledglings all survived to independence (age 65 days). Of 15 chicks that disappeared between hatching and fledging, nine were last seen on the day of hatching, and the others were last seen on days 2, 4, 10, 15, 16 & 30. [Note that living chicks were seen every 3.6 ± 5.0 days; n = 384, range 0 - 41 days.] No study chicks were found dead, however, a juvenile Red-billed Gull *Larus novaehollandiae* regurgitated a pair of legs of a small snipe chick on the edge of the study area on 6 February 1984. Gulls rarely used the same habitat as snipe on the Snares Is, and so were unlikely to have been significant predators of chicks.

Three of 29 chicks (10.3%) that were banded in the nest survived to one year of age; 15 of 33 fledglings (45.5%) were found as one-year-olds. This compares with annual adult survival of about 83.3%.

In 1985-86 19 pairs produced 13 fledglings, of which four survived to age one year; in 1986-87 20 pairs produced 11 fledglings, of which four survived to age one year (Table 1.2).

Table 1.2. Breeding success of New Zealand Snipe on the Snares Islands over two breeding seasons. Sample sizes are given in parentheses.

	% pairs breeding	% eggs hatched	% chicks fledged	fledglings per pair	% survival to 1 year	1-year-olds per pair
1985-86	78.9 (19)	81.8 (22)	54.2 (24)	0.68 (19)	30.8 (13)	0.21 (19)
1986-87	85.0 (20)	75.6 (41)	42.3 (26)	0.55 (20)	36.4 (11)	0.20 (20)
TOTAL	82.1 (39)	77.8 (63)	48.0 (50)	0.62 (39)	33.3 (24)	0.21 (39)

Of nine two-egg nests of Chatham Island Snipe studied, seven (77.8%) hatched both eggs, eight (88.9%) hatched at least one egg, and one (11.1%) failed (deserted the day after an addled egg was ejected from the nest). The one egg incubated full term that failed to hatch was cracked and addled. Of the 18 eggs laid in nine nests, 15 (83.3%) hatched (a mean of 1.67 eggs per nest, and 1.88 eggs per successful nest).

Discussion

Snipe breeding systems

The breeding systems of New Zealand Snipe and Chatham Island Snipe were very similar (Table 1.1); both species occurred at high densities, and laid small clutches of eggs that were large in relation to female body-weight. Incubation was shared, and there was high hatching success. Chick weights increased at a similar rate, but Chatham Island Snipe chicks became independent when about three weeks younger than New Zealand Snipe chicks (Table 1.1).

Common Snipe occur at much lower densities than New Zealand Snipe and Chatham Island Snipe (Table 1.1; figure of 0.4 ± 0.7 pairs/ha for Common Snipe based on 21 estimates of density given by Tuck 1972 and references therein, and Green 1985b). The high density of New Zealand Snipe was associated with high annual survival of adults (83.3%). The highest estimate of survival for adult Common Snipe is 62.5% (Spence 1988).

Courtship feeding has not been recorded previously for any scolopacid (Lack 1940, Tuck 1972, Johnsgard 1981, Sutton 1981, Cramp & Simmons 1983). Although New Zealand Snipe pairs consorted together for up to 15 weeks before laying, courtship feeding was only seen in the last three weeks and was not directly associated with mating attempts. These observations suggest that courtship feeding of females by male *Coenocorypha* snipes evolved to decrease energy demands on the female during egg formation, rather than simply to maintain the pair-bond (see Cullen & Ashmole 1963, Royama 1966, Lack 1968, Nisbet 1973, Tasker & Mills 1981). The long interval between successive clutches laid by New Zealand Snipe that failed during their first breeding attempt also suggests that nutrient availability during egg formation was limiting. Common Snipe females that failed during their first breeding attempt relaid after 14 days (n = 5, range 11 - 19 days; Green 1988), compared with a mean of 36 days for New Zealand Snipe.

A small clutch size is characteristic of birds in environments with low food availability (Lack 1954, Stearns 1976). As New Zealand Snipe feed their young for up to six weeks, clutch size may be limited by the ability of parents to rear young (Winkler & Walters 1983) as well as the cost of egg formation (Lack 1954, 1968, Stearns 1976).

Common Snipe lay eggs that are only slightly smaller than expected for a 112 g charadriiform (Table 1.1; Rahn *et al*. 1975, Sæther *et al*. 1986), and these are laid only one day apart (Cramp & Simmons 1983). New Zealand Snipe eggs are 22.8% larger than expected for a 116 g charadriiform (Rahn *et al*. 1975). Large eggs are considered an adaptation to a poor or unpredictable food supply, as the young hatch more fully developed and/or with a large yolk supply to compensate for the low rate of food consumption following hatching (Martin 1987 and references therein). Large egg-size and low food availability may have been the cause of the long (three day) egg interval of New Zealand Snipe. The long egg intervals of passerines in Tasmania and south-east Australia have been attributed to low food availability during egg formation

(Thomas 1974, Woinarski 1985).

Large eggs take longer to hatch than small eggs (Rahn & Ar 1974, Sæther *et al.* 1986). Under the same incubation regime, New Zealand Snipe eggs would be expected to take 5.5% longer to hatch than Common Snipe eggs (Equation 1 in Rahn & Ar 1974). However, New Zealand Snipe had an incubation period 15.8% longer than Common Snipe, even though incubation was shared (100% constancy). A female New Zealand Snipe incubating by herself (analogous to incubation by Common Snipe) took about 38 days to hatch an egg, twice as long as Common Snipe.

Single-sex incubation is associated with lower incubation constancy, as the incubating parent must leave the nest to feed (Løfaldli 1985, Chapter 2). The low incubation constancy (c.70%) and long incubation period of female New Zealand Snipe incubating by themselves suggests that food availability on the Snares Islands was insufficient for the short foraging excursions required to keep eggs above physiological zero temperature (Løfaldli 1985, Kålås 1986). Shared incubation by New Zealand Snipe (95% of pairs) may be interpreted as an adaptation to low food availability, as the eggs were maintained above physiological zero temperature, yet both parents had up to 50% of the day in which to forage (cf. c.22% for an incubating female Common Snipe; Green *et al.* submitted MS).

Although New Zealand Snipe chicks were about 37% heavier than Common Snipe chicks on hatching, their rate of growth was 37% slower (Fig. 1.3; Table 1.1). New Zealand Snipe chicks took about 1.5 times longer to fledge and about three times longer to reach independence as Common Snipe chicks (Table 1.1). Lack (1968), Case (1978) and Ricklefs (1968, 1983) argued that growth rates are adjusted to the amount of food that is available. Low body-weights of adult New Zealand Snipe during the prolonged period of parental care provide direct evidence of energy limitation during chick-rearing.

The durations of incubation and fledging periods are positively correlated (Lack 1968: 292, Drent 1975); chicks that take longer to develop before hatching also take longer to fledge. The growth rates (K_G) of *Coenocorypha* snipes are exceptionally low for birds with an incubation period of 22 days (Figure 2 in Drent 1975). The rate of development determines the period during which young are vulnerable to predation (Lack 1968). As predation of snipe chicks is rare on the Snares or Rangatira Islands, growth rates may be lowered to an energetic optimum. However, Ricklefs (1969, 1973) has argued that growth rate and mortality are not correlated and that in most species growth rates are driven to a physiological maximum.

Hatching success for New Zealand Snipe and Chatham Island Snipe was far higher than Green (1988) found for Common Snipe. The main causes of nest failure for Common Snipe in his study were egg predation, trampling of nests by livestock and flooding (Green 1988); none of these factors was present on the Snares Islands or Rangatira Island during this study. The main cause of nest failure for both New Zealand and Chatham Island Snipes was desertion. Of the seven New Zealand Snipe clutches deserted over five years (17.5% of nests), two were during the severe El Niño event of 1982-83 (Chapter 4), one was in a nest with female single-sex incubation (Chapter 2), one was laid and deserted before the annual summer increase in prey availability in early December 1986, and three were deserted following a decline in prey abundance in mid February 1987 (Chapter 5). Thus all seven desertions may have been due to inability of the incubating birds to obtain sufficient food. Desertion rates of Common Snipe were much lower (6.7%; data from Green 1988). The higher desertion rates of *Coenocorypha* snipes suggest that incubating birds were more subject to food shortages than Common Snipe.

There are no data available on the number of chicks reared per year by Common Snipe. Green (1988) used estimated chick mortalities of 6 - 12% per day to model relaying frequency of Common Snipe, and estimated that each female hatched between four and eight eggs. Using these figures, each breeding female would have produced between 0.3 and 2.2 fledglings per year. These figures encompass the 0.6 fledglings per year reared by New Zealand Snipe pairs on the Snares Is. The low mortality of New Zealand Snipe chicks (c.1.6% per day until fledging) was presumably due to the almost total absence of predation.

Environmental constraints on breeding of *Coenocorypha* snipes

Ten features of the breeding system of New Zealand Snipe indicate that the population on the Snares Is is severely limited by food availability during the breeding season. Several of these features have not been recorded for other scolopacids, suggesting that they arose as functional responses to recent environmental conditions, rather than being plesiomorphic traits. Compared with Common Snipe, New Zealand Snipe have courtship feeding, large eggs in relation to female body-weight, a long egg interval, a small clutch, shared incubation, a long incubation period in relation to egg size, slower chick growth rates, a long period of chick dependence, a higher nest desertion rate, and a long relaying interval following breeding failure. At least eight of these features are shared by the less studied Chatham Island Snipe. The only aspects of *Coenocorypha* life histories that appear, at first glance, to run counter to this argument are their high population densities, high hatching success and high survival rates; I suggest that these features are due to the absence of predation.

Other shorebirds breeding in southern temperate latitudes lay small clutches (Maclean 1972, Winkler & Walters 1983), but it is not known whether their breeding systems share other features with *Coenocorypha* snipes. Why are the breeding systems of New Zealand snipes (and, presumably, other southern hemisphere shorebirds) limited by food to a greater extent than holarctic shorebirds? A positive correlation between latitude and clutch size has long been recognised for northern hemisphere birds (Lack 1968, Klomp 1970, Ricklefs 1980). Small clutches of tropical birds are thought to be due to reduced seasonality in the tropics (Ashmole 1963, Ricklefs 1980, Winkler & Walters 1983). Species living in a stable environment are expected to be at or near carrying capacity (Cody 1966) and hence to invest reproductive energy into producing fewer, more competitive offspring.

The correlation between latitude and clutch size does not apply to New Zealand birds (Oliver 1955, Cody 1966, Niethammer 1970). The New Zealand climate is highly moderated by the southern ocean, with mild winters and cool, protracted summers (Hurnard 1978). Most New Zealand plants have year-round leaf production (Dumbleton 1967, Wardle 1978) and insect diapause is rare (Roberts 1978). Reduced seasonality in food availability is likely to increase winter survival of non-migratory shorebirds, and create intense competition for food resources during the breeding season. Reduced climatic seasonality may be the driving force behind small clutch sizes of southern hemisphere shorebirds (see also Ricklefs 1980, Woinarski 1985).

Small oceanic islands are very stable environments (Cody 1966, Stamps & Buechner 1985). Annual mean monthly temperature range on the Snares Islands is about 6.6°C (New Zealand Meteorological Service 1972), and is about 7.1°C on the Chatham Islands (Thompson 1983). The absence of predators of snipe on Snares and Rangatira Is has permitted snipe to occur at very high population densities; these high densities in a stable environment are likely to result in severe food limitation during the breeding season. I suggest that the breeding systems of New Zealand and Chatham Island Snipes have been constrained through intense intraspecific competition for a limited food supply.

Chapter 2

Flexible incubation system and prolonged incubation in New Zealand Snipe.

Wilson Bulletin 101 (1989): 127-132.

Introduction

Shorebirds of the family Scolopacidae (Charadriiformes) have a wide variety of mating systems (Jenni 1974, Pitelka *et al.* 1974, Pienkowski & Greenwood 1979). Monogamy, with shared incubation of the same clutch, is presumed to be the primitive mating system (Jenni 1974, Pitelka *et al.* 1974). However, in a number of species, male or female emancipation has led to uniparental care by either sex (Hogan-Warburg 1966, Norton 1972, Pitelka *et al.* 1974, Reynolds 1987), or both sexes incubate different clutches simultaneously (Parmelee & Payne 1973, Hildén 1975, Pienkowski & Greenwood 1979). Species with shared incubation of the same clutch keep the eggs covered almost continuously (Norton 1972), while shorebirds with single-sex incubation have an incubation constancy of 80-90% (Drury 1961, Parmelee 1970, Norton 1972, Cartar & Montgomerie 1985, Løfaldli 1985), as the incubating parent must divide time between nest attentiveness and food gathering (White & Kinney 1974, Løfaldli 1985). The incubating parent may take frequent foraging excursions which are short enough to maintain the eggs above physiological zero temperature (Løfaldli 1985, Kålås 1986), or it may take longer feeding trips, allowing the eggs to cool (Lill 1979).

New Zealand snipe *Coenocorypha* are typically monogamous, with shared incubation (Chapter 1). However, in a study of 20 pairs of Snares Island Snipe *C. aucklandica huegeli* over six years, I observed simultaneous polygyny by two different males in separate field seasons. The remaining males were all monogamous. Here I document the incubation system associated with polygyny (three nests) and compare it with that of typical, monogamous pairs (37 nests). The polygynous males devoted almost all of their parental effort to one nest. The additional females incubated by themselves, thus the incubation system became more like that found in other snipes (i.e., female single-sex, intermittent incubation; Tuck 1972, Cramp & Simmons 1983, Løfaldli 1985). Both solo-incubating females paired monogamously and shared incubation with their mates in previous seasons.

Study area and methods

Snares Island Snipe were studied in *Olearia* forest on the Snares Islands (48°01′S 166°36′E) south of New Zealand. Six visits to the study area were made each summer beginning in 1982. The most intensive work was carried out from 2 Nov. 1985 to 10 Mar. 1986, and from 22 Oct. 1986 to 20 Feb. 1987. All adult snipe within the 7.5 ha study area were individually colour-banded for the duration of the study. Territories and home ranges of snipe were plotted in relation to a 20 m grid system during daily surveys of the study area. Pairs were identified by mating, courtship feeding, or prolonged consorting. Snipe were sexed by measurements during handling (females are larger; unpublished data) and by sex-specific calls and displays after marking. Most breeding attempts were detected during incubation; laying dates for nests with shared incubation were recorded directly, or calculated from hatching dates by subtracting 22 days for incubation (determined from three nests) and three days for egg interval (determined from five nests; the typical clutch is two eggs). Incubation length was taken as the time from laying of the second egg to hatching of either egg. Eggs, when found, were weighed to 0.5 g and measured to 0.1 mm. Fresh egg masses were obtained before incubation for 9 eggs. For nests with single-sex incubation, fresh egg masses were calculated using the equation: $M = 0.000526 \times L \times B^2$, where M is initial egg mass (g), L is egg length (mm) and B is maximum egg breadth (mm). The constant was obtained empirically from the 9 fresh eggs mentioned above. Nests were checked at least once daily, and more frequently during hatching. If no bird was sitting, the eggs were touched to determine whether they were warm. Hides were erected near four nests (one with female single-sex incubation), and five continuous 24 h watches were undertaken. A chart recorder, light beams and photo-electric cells were used to record incubation constancy at two nests with shared incubation in November-December 1987. Daily air temperatures were taken within the study area.

Results

Case 1

Of 20 territory-holding males in the study area in 1985-86, one (Male A) had two mates simultaneously. Initially he courted only Female A, his mate of the previous three seasons. Female A was suspected to have commenced incubation about 24 Nov., as she was not seen during surveys of the study area after 23 Nov.; her nest (Nest 1) was not found until 5 Dec. The male commenced courting Female B on 22 Nov., the day after the estimated first egg-laying date of Female A. Male A and Female B shared incubation at Nest 2, which was found on 9 Dec. Both eggs in Nest 2 hatched on 21 Dec., giving estimated laying dates of 27 and 30 Nov.

Female A at Nest 1 incubated by herself. No other birds were seen during 57 spot checks over 28 days at Nest 1. Female A frequently left the nest for extended periods to feed (over 100 min on one occasion), during which the eggs cooled to ambient temperature (7.5 - 19.0°C). Egg mass loss at this nest over 23 days averaged 69% of that found for nests with shared incubation (Table 2.1). Using my equation to obtain fresh egg weights, and assuming a constant rate of water loss (Drent 1970, Rahn & Ar 1974), it appeared that incubation at Nest 1 started about 26 Nov. (cf. 24 Nov. determined by behaviour). Water loss probably occurred mainly during active incubation in the humid environment of the Snares Islands, as a fresh egg which was deserted had lost no measurable mass after seven days in the nest; this suggests that incubation constancy at Nest 1 was approximately 69%. Both eggs in Nest 1 developed fully, although one chick died while hatching. Hatching occurred 28 days after the nest was found, and 37 - 39 days after the estimated start of incubation, which is 68 - 77% longer than normal. The surviving chick from Nest 1 and both chicks from Nest 2 were raised to fledging.

TABLE 2.1

INCUBATION DETAILS FOR NEW ZEALAND SNIPE UNDER TWO DIFFERENT INCUBATION REGIMES

Incubation regime	Shared	Solo		
	N = 37	Case 1 (Nest 1)	Case 2 (Nest 4)	Case 3[a] (Nest 5)
Clutch size	2	2	2	2
% Female incubation	38[c]	100[d]	99.9[f]	100[g]
Incubation constancy (%)	100[c]	ca 69[e]	72[f]	—
Egg mass loss (gd^{-1})	0.182	0.125	—	—
Incubation length	22	37–39	Failed	Unknown
Male reproductive success[b]	≤2	3	≤4[h]	
Female reproductive success	≤2	1	≤2[h]	

[a] For first 5 days only, after which incubation was shared.
[b] Measured as number of young raised to fledging in one breeding season.
[c] Obtained from 24-h recordings at 5 different nests.
[d] From 57 nest checks over 28 days.
[e] Estimated from rate of egg mass-loss (see text).
[f] From two 24-h watches.
[g] From 7 nest checks over 5 days.
[h] Cases 2 and 3 refer to the same male and female in the same breeding season.

Case 2

Male A and Female B disappeared between Mar. and Oct. 1986. In 1986-87 Male B from an adjoining territory defended an enlarged area combining both males' territories. He courted three females: Female A, the solo-incubating female of 1985-86; Female C, his mate from 1985-86; and Female D, a female from another previously adjoining territory, whose mate had also disappeared. Male B was seen mating with Female A on 13 and 14 Nov. Female A laid eggs on 22 and 25 Nov. (Nest 3) and shared incubation with Male B; the eggs hatched on 17 and 18 Dec.

Between incubation shifts at Nest 3, Male B courted Females C and D, and was seen mating with Female D on 26 and 27 Nov. Female C probably laid eggs soon after 15 Dec., when she was captured and determined (by palpation) to be near egg-laying condition. Female C is presumed to have deserted early in incubation, since she was paired with another male by 21 Jan.

Female D was found incubating two eggs (Nest 4) on 27 Dec., although she was suspected (by behaviour and egg masses) to have commenced incubation about 16 Dec. Male B was caring for a nine-day-old chick from Nest 3 when Nest 4 was found. Female D incubated largely by herself for the next 11 days, although the male visited the nest up to four times a day and incubated for short periods (e.g. a five min shift during a 24 h watch on 30 Dec.). The female fed for long periods (up to 11 h 55 min) after replacement at the nest by the male; but as the male left the nest soon after the female, the eggs were uncovered for much of this time. Incubation constancies during 24 h watches at Nest 4 on 30 Dec. and 5 Jan. were 60% and 83% respectively. Nest 4 was deserted about 7 Jan., about 22 days after incubation started. Both eggs contained half-developed embryos; I do not know if the embryos were alive when the nest was deserted.

Case 3

Female D relaid in a new nest (Nest 5) on 5 and 8 Feb. 1987, and incubated solo for the next five days. Male B continued to care for his 7.5-week-old chick from Nest 3 until 13 Feb., when he commenced his full share of incubation at Nest 5. Incubation at Nest 5 was continuing when I left the island on 20 Feb., so Male B potentially fathered four chicks during the breeding season (cf. a maximum of two for a monogamous male).

Discussion

Other shorebirds have flexible mating and incubation systems. Spotted Sandpiper *Actitis macularia* (Hays 1972, Maxson & Oring 1980) and Eurasian Dotterel *Charadrius morinellus* (Kålås 1986) usually have male single-sex, intermittent incubation, but females occasionally assist. Incubation constancy at Eurasian Dotterel nests where both sexes incubated was similar to nests where the male incubated alone; no decrease in incubation length with shared incubation was found (Kålås 1986). Solo incubating male Wilson's Plovers *Charadrius wilsonia* increased their time on the nest significantly, but there was a decrease in total incubation constancy compared with nests where incubation was shared (Bergstrom 1981). There was no concomitant increase in incubation length with single-sex incubation in Wilson's Plovers, possibly because the change in incubation pattern occurred late in incubation, and the ambient temperatures were much higher than on the Snares Islands (Bergstrom 1981). Lessells (1983) experimentally induced extended, successful incubation by one parent in Kentish Plover *Charadrius alexandrinus*, analogous to the situation for New Zealand Snipe. Warriner *et al.* (1986) also recorded successful single-parent incubation by Kentish Plovers, for up to 10 days (by one male) and 7 days (one female), but this occurred only if the mate deserted after the 16th day of incubation. Erckmann (1983) found that neither males nor females were able to incubate alone in Western Sandpiper *Calidris mauri*.

New Zealand Snipe incubating by themselves did not achieve incubation constancies of other scolopacids with single-sex intermittent incubation (80-90%; Norton 1972, Cartar & Montgomerie 1985, Løfaldli 1985), although solo incubating females did increase the time spent at the nest compared with females at nests with shared incubation (Table 2.1). Eggs cooled to ambient temperature during feeding excursions, and did not remain above physiological zero temperature as found during the shorter excursions of shorebirds with single-sex incubation (Løfaldli 1985, Kålås 1986). Decrease in incubation constancy at nests with single-sex incubation caused a concomitant increase in incubation length. Delayed development is also the main effect of egg neglect in other birds (Boersma & Wheelwright 1979, Boersma 1982 and references therein, Murray *et al.* 1983, Sealy 1984). However, increase in incubation length in New Zealand Snipe resulted from a change in incubation regime rather than by periods of egg neglect within the normal incubation pattern (as occurs in all other species with variable incubation length; see references above).

Female New Zealand Snipe incubating by themselves had low hatching success. Males benefitted from emancipation as additional breeding opportunities increased their reproductive success compared with monogamous males. However, male emancipation was rare, and female single-sex incubation was only observed for two of 43 female-years. The change from shared to single-sex incubation resulted in a decreased incubation constancy and delayed embryonic development, with one female successfully hatching an egg after an incubation length 68 - 77% longer than normal.

Chapter 3

Social constraints on access to mates in a high density, non-migratory wader population.

Abstract

A colour-banded population of New Zealand Snipe *Coenocorypha aucklandica* was studied on the Snares Islands over six breeding seasons. Snipe occurred at densities up to 11.5 birds/ha. Up to 47% of males and 30% of females were excluded from breeding each year, although they were tolerated within breeding territories. Breeding adults were highly faithful to their territories and mates regardless of previous breeding success. About 83% of adults were recovered in the study area the year after banding. No males moved to different territories, and only 11% of females moved, all to adjacent territories. Less than 9% of breeders changed partners between years if their previous mate was still present.

Territory area was not influenced by intruder density; in years of high population density a higher proportion of birds was excluded from breeding. Nonbreeding adults obtained a territory or mate only if a territorial bird died. Prior residence was an important factor in acquiring a territory both within and between breeding seasons. Mortality was density-dependent, and a relatively constant proportion of nonbreeding birds was assimilated into the breeding population each winter.

New Zealand Snipe were faithful to their natal area; 46% of fledglings were recovered subsequently in the study area. There was no sex bias in return rates, but females tended to disperse slightly further than males. About 11% of males and 57% of females bred as one-year-olds. Young males were prevented from breeding by a large pool of nonterritorial males. No cases of inbreeding were recorded.

Introduction

Dispersal patterns of birds and mammals are closely linked with social structure (Greenwood 1980, Oring & Lank 1984). Greenwood (1980) concluded that sex-biased dispersal was driven largely by reproductive enhancement through increased access to mates or resources and the avoidance of inbreeding. In birds, where the predominant social system involves resource defence by males, females tend to disperse further than non-migratory members of the family breed in the southern hemisphere (Hayman *et al.* 1986). The New Zealand Snipe *Coenocorypha aucklandica* is a non-migratory wader that is now confined to three small oceanic island groups, each with an endemic subspecies (Hayman *et al.* 1986). New Zealand Snipe on the Snares Islands occur at high densities and many birds are unable to obtain a territory or mate (Chapter 1). This paper describes social structure, dispersal patterns and mortality rates in a colour-banded population of New Zealand Snipe on the Snares Islands, focussing on factors that limit access to mates. Differences in breeding dispersal patterns between New Zealand Snipe and other scolopacids are discussed with regard to the constraints imposed by a sedentary habit and intense competition for mating opportunities.

Study area and methods

A colour-banded population of New Zealand Snipe was studied on the Snares Islands Nature Reserve (48°02′S 166°36′E) during all breeding seasons from 1982-83 to 1987-88. Fieldwork was carried out between September and March, which encompassed all egg-laying and early stages of chick-rearing (Chapter 1). A total of 541 days of observations was made, including 64 days by G.J. Eller in 1983-84, when I was absent from the island.

The study area was situated just north of the Biological Station on Main (North East) Island and was marked out in a 20 m grid. For the first two field seasons the study area was about 4 ha in area, but it was extended to 7.5 ha in 1984-85. About 61% of the study area was under a tight 6 - 10 m canopy of *Olearia lyalli*, with some *Brachyglottis stewartiae*; 28% was open, and 12% was under a 2 - 4 m canopy of *Hebe elliptica*. Ground cover was a mosaic of bare peat (32%) and tussock (29%, mainly *Poa tennantiana*), with smaller areas of fern (13%, mainly *Polystichum vestitum*), swards of *Callitriche antarctica* and *Crassula moschata* (10%), bare rock (6%), mud (5%), and *Stilbocarpa robusta*, penguin colonies and open water (2% each).

Adult snipe were captured with a handnet during the day, or with a spot-light and handnet at night. All 21 - 64 adult snipe resident in the study area each year were individually colour-banded (total = 93) and assigned to one of five social classes (see Results) on the basis of intraspecific interactions. Adults were sexed by measurements and sex-specific displays (unpubl. data). Locations of marked birds were recorded in relation to the grid system during daily surveys of the study area. Territory boundaries were identified by observing territorial disputes and by plotting sightings of calling males during the courtship and incubation stages of the breeding cycle. Territory areas (and the area of zones of overlap between years for each male's territory) were estimated with a polar planimeter (mean of three replicates from each of two pole positions). Pairs were identified by prolonged consorting, courtship feeding, mating or attendance at the same nest.

Forty-five nests were found in the study area (Chapter 1). Chicks were banded in the nest (n = 29) or while accompanying an adult (n = 69). An adult known to have had a dependent chick was considered to have failed if the adult was seen three or more times unaccompanied by a chick, and the chick was not seen subsequently. Areas of suitable habitat in a band 400 m wide around the study area were searched regularly (every 2 - 3 days) for banded snipe. Snipe seen by expedition members elsewhere on the island (maximum of 2.3 km from the study area) were routinely checked for bands.

Measurements are given as mean ± s.d. unless otherwise stated.

Results

Social structure

Territory defence by New Zealand Snipe was performed solely by males. At the start of each breeding season the study area was divided into contiguous, non-overlapping territories of 0.078 - 0.630 ha (0.268 ± 0.121 ha, n = 82). Males defended their territories by Loud Calling (Appendices 2 & 4) and, occasionally, by fighting (Miskelly 1984). Those males that maintained exclusive territories at the start of a breeding season (November) were defined as alpha males, and comprised 53 - 83% of the resident males each year (Table 3.1).

Territory ownership by a male was a prerequisite for obtaining a mate, but 7 of 82 alpha males (9%) did not have mates for one breeding season. The remaining alpha males were monogamous, with the exception of one simultaneously polygynous male in each of four years (Chapters 1 & 2). All mates of alpha males at the start of a breeding season were defined as alpha females, and comprised 70 - 91% of the resident females each year (Table 3.1). The remaining 9 - 30% of females were referred to as beta females.

Table 3.1. Density of snipe (birds/ha) in the study area 1982-83 to 1987-88. For each season, densities were calculated for only those birds whose entire territory or home range was contained within the artificial boundaries of the study area, hence areas given in the table are slightly less than for the full study area, i.e. 4 ha for 1982-84 and 7.5 ha for 1984-88.

Year	Area (ha)	Males				Females			Total
		Gamma	Beta	Alpha	Total	Beta	Alpha	Total	
1982-83	3.91	0.77	1.28	2.56	4.60	0.77	1.79	2.56	7.16
1983-84	3.91	-	0.77	2.81	3.58	0.51	1.28	1.79	5.37
1984-85	5.59	0.18	0.89	3.04	4.11	0.72	2.15	2.86	6.98
1985-86	5.59	0.54	2.68	3.58	6.80	1.25	3.40	4.65	11.45
1986-87	5.28	0.38	1.14	3.79	5.30	0.38	3.98	4.36	9.66
1987-88	5.16	0.19	0.58	3.68	4.46	0.39	3.88	4.26	8.72

During courtship and incubation, alpha males defended their territories against all other Loud Calling males. Silent males (and all females) fed unchallenged within any territory, although alpha males, before incubation commenced, chased any male approaching within 2 m of the alpha female. Forty-four different nonterritorial males were seen within alpha males' territories on 641 occasions; on 68 occasions the intruder was seen within 10 m of the resident alpha male. Alpha males attacked or chased 14 intruders that called, plus a further two that approached the alpha female; 52 intruders were ignored or displayed to, without being attacked or chased from the territory.

Following hatching, alpha males attempted to maintain their territory while caring for one of the two chicks, but most were unable to evict other Loud Calling males, and after 1 - 2 days devoted all their time to chick-rearing. Only one alpha male successfully defended his territory while raising a chick (the simultaneously polygynous male in 1986-87; Chapter 2). Territories of the remaining 24 alpha males with dependent young were usurped by one or more previously nonterritorial males, each of which then maintained an exclusive territory. A male that did not hold a territory in November, but who challenged an alpha male and/or claimed a territory while the previous owner was raising a chick, was classified as a beta male. Beta males that obtained territories late in the season invariably had home ranges that had overlapped with the previous owner's territory, i.e. prior residency was a prerequisite for obtaining a territory within a breeding season.

Beta males comprised 13 - 40% of the resident male population each year (Table 3.1). After obtaining a territory, beta males courted any resident female that did not have a dependent chick - either an alpha female that had lost her chick (n = 5), or a beta female (n = 5). One beta male in 1985-86 and another in 1986-87 obtained mates that subsequently laid; both females were alpha females whose original mates were still raising a chick.

The remaining 0 - 17% of males each year, termed gamma males, did not have fixed home ranges and did not attempt to gain territories (Table 3.1).

Alpha males that lost their dependent chick immediately reclaimed their former territory (n = 16) and courted any resident female that did not have a dependent chick - usually their previous mate (n = 12, 6 of which laid again), but occasionally another alpha female (1, which laid) or a beta female (2, 1 of which laid).

Movement between social classes and age of first breeding

Movement between social classes occurred in one direction only, although 25 - 33% of the beta status birds of both sexes retained that status for two breeding seasons (Table 3.2). All gamma males were probably one-year-old; the beta male class was comprised of almost equal numbers of one- and two-year-olds. All males aged three years or older were alpha males. Two one-year-old males defended territories (alpha male status) but neither obtained a mate.

The youngest male recorded breeding was a one-year-old beta male; the same bird also bred as an alpha male at age two- and three-years. The only other known-age male breeders were a beta male at age two-years and an alpha male at age three-years.

Females entered the breeding population younger than did males: 71% were paired at one-year-old (Table 3.2). The beta female class was comprised of similar numbers of one- and two-year-olds. All females aged three years or older were alpha females.

Table 3.2. Movement of snipe through social classes. Social status in the first year (Year N) is given across the top of each column; social status in the following year (Year N + 1) is given in each row. For example, social status was determined for 12 one-year-old males that had been banded as chicks: 2 were gamma males, 8 were beta males and 2 were alpha males.

A. Males		Year N			
		Chick	Gamma	Beta	Alpha
	Gamma	2	-	-	-
Year N+1	Beta	8	1	6	-
	Alpha	2	2	18	76

B. Females		Year N		
		Chick	Beta	Alpha
Year N+1	Beta	4	3	-
	Alpha	10	6	65

Once a bird of either sex attained alpha status, it retained that status until it disappeared from the study area (presumed dead).

Four of seven one-year-old females bred (57%), compared with one of nine one-year-old males (11%)(Fisher's exact test, P = 0.1058). Three females first bred as two-year-olds, and two as three-year-olds.

Natal philopatry, dispersal and inbreeding

In birds, natal philopatry is usually estimated by banding a large number of chicks, then recording the number of each sex subsequently found as breeders in the study area (Oring & Lank 1984). If natal dispersal is low, an estimate of natal philopatry may simply reflect sexual differences in prebreeding survival. However, prefledging mortality in shorebirds is usually very high (e.g. Green 1988, Thompson & Hale 1989), therefore the age at which chicks are marked greatly influences estimates of natal philopatry and survival to breeding age (Thompson & Hale 1989).

Of 98 snipe chicks handled on the Snares Islands, 29 were banded on the day of hatching (usually within the nest bowl) and 69 were banded at 1 - 78 days old. Three (10.3%) chicks banded in the nest were recovered in or near the study area at breeding age (one or more years old); 26 (37.7%) chicks banded away from the nest were recovered at breeding age. Chicks banded away from the nest were more likely to be recovered in subsequent years than chicks banded on the day of hatching (X^2 = 7.32, P = 0.007), because most nestling mortality occurred within a day of hatching (Chapter 1 and Table 3.3). Late hatching chicks were just as likely to be recovered in subsequent years as early hatching chicks (Chapter 1). About 46% of fledglings were found as one-year-olds.

Table 3.3. Sightings of known-age adult snipe in or near the study area in relation to age of last capture (or sighting) as a chick. Recovery rates at age one year did not differ for early and late hatching chicks (Chapter 1).

Age at last capture (days)	No. of chicks captured	No. recovered at age 1+ years	% recovered
0 (in nest)	16	1	6.3
1 - 20	20	4	20.0
21 - 40	16	6	37.5
41 - 60	23	7	30.4
61 - 80	11	5	45.5

The 29 one-year-olds recaptured in or near the study area were divided equally by sex: 14 males (14% of chicks banded) and 15 females (15%). Natal dispersal distances of the sexes was estimated by measuring the distance between the centres of natal and first own-territories for 17 known-age snipe. Nine females moved 202 ± 87 m (range 80 - 350 m), significantly further than eight males (113 ± 86 m; range 0 - 260 m) (t_{15} = 2.14, P = 0.049). Note that territories averaged about 58 m in diameter.

Sex-biased natal dispersal is often claimed to be an inbreeding avoidance mechanism (Bischof 1975, Packer 1979, Greenwood 1980).

Although natal dispersal distances of male and female snipe overlapped, sibling-sibling inbreeding was unlikely to occur due to the low probability of two siblings of opposite sex surviving to breeding age (about 1.4%) combined with the low probability of the members of an alpha pair both dying at the time when the two siblings were attempting to obtain their respective territories (about 2.2%). Parent-sibling inbreeding was also unlikely due to the low probability of an alpha status bird dying the same year that its same-sex offspring was looking for a territory (about 2.4% for males and 1.9% for females).

No instances of inbreeding were recorded during the six years of this study. However, only two pairings were recorded where both birds were of known parentage, along with 15 pairings where one bird was of known parentage. Adults of unknown parentage were either raised outside the study area (n = 40) or were adults when the study began (n = 35).

Breeding dispersal and survival of adults

Alpha males and alpha females that held territories within the study area were never subsequently found on territories outside the study area. Estimated breeding site fidelity (Table 3.4) is probably an accurate estimate of the mean annual survival rates of breeding males and females. A few nonbreeders (beta and gamma status) banded in the study area were subsequently found on territories up to 180 m outside the study area (see Natal philopatry), but recovery rates of these birds (Table 3.4) are also considered accurate estimates of between-year survival, as none was found further than 180 m from the study area. No snipe of any age was seen further than 350 m from where it was banded.

Social status had no effect on the probability of a bird being recovered in the subsequent year (Table 3.4). Mean adult breeding site fidelity (= survival) was 83.3%.

Territory and mate fidelity

Alpha males never lost their territory-holding status between seasons (n = 76; Table 3.2). To determine whether alpha males changed territory location between seasons, I compared territory overlap between consecutive years. If a male retained the same territory in consecutive years, overlap would be 100%; if a male moved to a new part of the study area, overlap would be zero. Territory maps for the same male in consecutive years were obtained for 23 different males (1 - 3 cases each,

Table 3.4. Sightings of adult snipe of known breeding status in or near the study area one year after banding. Birds were counted more than once if present in the study area for two or more years. All between group comparisons of return rates were nonsignificant ($P > 0.05$).

	No. present Year N	No. present Year N+1	%	χ^2	P
Alpha male	78	64	82.1	0.16	0.69
Beta & gamma males	43	34	79.1		
Alpha female	64	56	87.5	0.21	0.65
Beta female	18	15	83.3		
Total male	121	98	81.0	1.10	0.30
Total female	82	71	86.6		
Total	203	169	83.3		

total = 44 cases). Mean percent overlap between consecutive years was 53.1 ± 19.1% (range 9.9 - 94.7%). Once a male obtained a territory, he always retained at least 10% of that territory in the subsequent year; no male shifted his territory entirely during the six years of the study.

There were 50 cases where the mates of territorial male Snares Island Snipe were known for two consecutive seasons. Of 47 cases where both members of the pair were still present in the study area in the second season, 43 (92%) males retained the same partner as at the start of the previous breeding season, and four (8.5%) had new mates. The four females that changed mates all moved to adjacent territories; three had bred successfully the previous year.

Breeding success the previous year did not affect mate fidelity. There were 39 cases where both members of a pair were alive in the subsequent season, and where it was known whether the pair had succeeded in raising at least one chick to a minimum age of five days old. Eighteen of 21 successful pairs, and 17 of 18 failed pairs remained together for the second season (χ^2 = 0.803, n.s.). One pair that failed for three consecutive years was still together the following year.

A female whose mate disappeared between breeding seasons either paired with the male that claimed the vacant territory (n = 8) or moved to an adjacent territory (n = 2).

Effect of population density on territory size

If territory size is determined by intruder pressure, there should be a strong negative correlation between the density of potential territory holders and territory area (Krebs 1971, Myers *et al.* 1979). In contrast, if a territory holder defends an area that contains sufficient resources (e.g. space, food, nest sites) to obtain a mate and raise young, then territory area should vary independently of intruder pressure (Hinde 1956). A third possibility is that minimum territory size is set by resource abundance, but at low intruder pressures territory holders may defend as large an area as possible (Verner 1977, Parker & Knowlton 1980).

There was no clear relationship between the density of male snipe in the study area and mean territory area (Fig. 3.1). Although there was a slight tendency towards larger territories at low male densities (r_4 = -0.102, n.s.), it appears that territory size was not controlled solely by intruder pressure. Mean territory area did not drop below 0.24 ha, which suggests that a minimum resource requirement determines territory size at high male densities. In other words, during years of high male densities, beta and gamma males should find it harder to obtain a territory than in years of low male density.

How males obtained territories

There were three potential ways that beta or gamma males could obtain a territory: 'replacement' of an alpha male that died, 'eviction' of an alpha male by fighting, or by forming a new territory between two or more previously contiguous territories ('intercalation'). As already noted, every alpha male retained his territory until he disappeared (presumed dead); eviction was never observed. However, if alpha males were killed or severely injured during fights with beta males, it would be impossible to distinguish eviction from replacement without observing the conflict. One fight between an alpha and beta male continued for over 63 min, but all 'prehatch' contests seen were won by alpha males. One alpha male was found dead (within his territory); I was not able to determine the cause of death. As no vanquished alpha males were observed, and mortality rates for males were no different than for females (Table 3.4), it is likely that alpha males retained their territories until death from causes other than fighting.

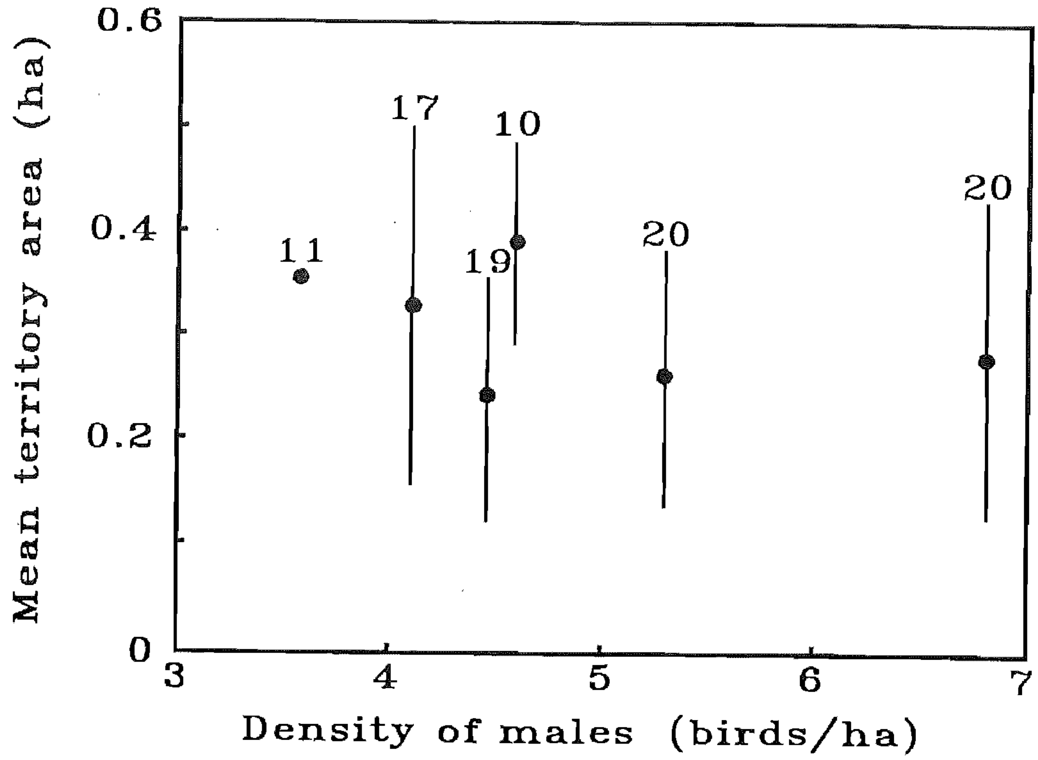

Figure 3.1. The relationship between total male density and mean territory area. Error bars represent one standard deviation of the mean. Numbers above each estimate give the number of territories that the estimate was based on. Territory boundaries were not determined accurately in 1983-84, and so the mean territory area was calculated by dividing the total area occupied by the number of alpha males present, hence there was no estimate of variability for that year.

Eighteen males attained alpha status (i.e. gained a territory) during this study: 12 by replacement and six by intercalation (Table 3.5). Twelve of the males that claimed new territories, including all six that obtained territories by intercalation, previously had home ranges that overlapped with their new territory (Table 3.5). To obtain a territory by intercalation required significantly longer prior residency than to acquire a territory by replacement (X^2_2 = 7.2, P = 0.027). [This result should be used with caution, as four of the six cells in the contingency table contained values below 5; see Table 3.5, and Everitt 1977.] In every case (n = 6) where beta males had home ranges that overlapped with a territory that became vacant, one of them took control of the territory. If there was no 'resident' beta male the territory was absorbed by surrounding alpha males (n = 4) or taken over by a male not previously resident there (n = 6).

Table 3.5. How new alpha males obtained their territories. "Eviction" = the previous territory owner was forced to abandon the territory. "Replacement" = the previous owner disappeared (probably died). "Intercalation" = the new territory was formed between existing territories, i.e. neighbours shifted their territory boundaries to accommodate the new territory.

Years of prior residence as a beta male	How the territory was obtained		
	Eviction	Replacement	Intercalation
0	0	6	0
1	0	6	4
2	0	0	2
Total	0	12	6

All males attempting to obtain a new territory were constrained by alpha male mortality, as the number of territories in the study area was relatively constant at all male densities (Fig. 3.1). Even males obtaining territories by intercalation could do so only if an alpha male had disappeared from a nearby territory, allowing adjacent alpha males to adjust their territory boundaries. As alpha male 'mortality' was about 18% per annum, only 0 - 7 territories were available to the 3 - 18 beta and gamma males each year (Table 3.6). The relatively constant ratio between alpha male mortality and number of nonterritorial males (Table 3.6) suggests that mortality of snipe may have been density-dependent. A similar relationship was not apparent for alpha and beta females, possibly because of the low density of beta females (Table 3.1). Most new alpha females were one-year-olds or of unknown history.

Density-dependent mortality

The effect of density of conspecifics on overall mortality rates of New Zealand Snipe during the non-breeding season is shown in Fig. 3.2.

Table 3.6. Number of alpha males that disappeared between breeding seasons in relation to the number of beta and gamma males vying for territory ownership.

Year	Number of beta and gamma males present in the previous breeding season	Number of alpha males that disappeared	Proportion of beta and gamma males able to obtain a territory
1983	8	3	0.375
1984	3	0	0
1985	6	2	0.333
1986	18	7	0.389
1987	8	3	0.375

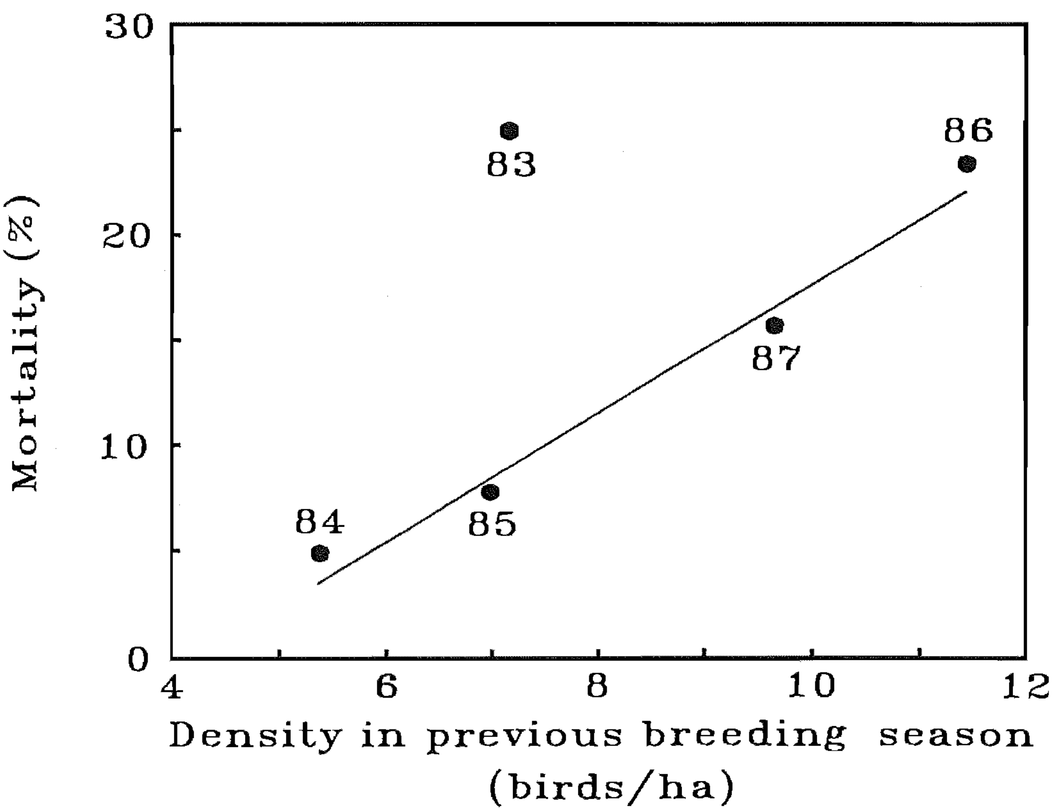

Figure 3.2. Density-dependent mortality in New Zealand Snipe. The very high mortality during the 1983 winter followed the severe 1982-83 El Niño Event. The regression line was fitted to the data for the remaining four years.

Mortality rates were, apparently, density-dependent; the one outlier was the high mortality in the winter following the severe 1982-83 El Niño event (Chapter 4). For the remaining four years, snipe density explained about 97% of mortality during the following winter ($r_2 = 0.98$, $P = 0.011$); this implies that there was intense intraspecific competition for a limiting resource, presumably food (see Chapters 1, 4 and 5).

Discussion

Territory defence

New Zealand Snipe on the Snares Islands had many life history features characteristic of insular vertebrates (Stamps & Buechner 1985): they occurred at high densities, adult and juvenile survival was high, clutch size was small and there was high parental investment per offspring (Chapter 1), onset of breeding was delayed (at least for males) and alpha males accepted subordinate (beta and gamma) males on their territories.

The presence of beta and gamma males within alpha males' territories appears inconsistent with evidence that New Zealand Snipe were food limited during the breeding season (Chapter 1). If food within a territory is a limiting resource, why share it with unrelated conspecifics? Alpha males maintained contiguous territories that included all suitable habitat within the study area; there were no interstices between territories, and no dispersal sinks (sensu Emlen 1979) for nonterritorial birds to occupy. Given that nonterritorial birds had no choice but to intrude into established territories, they could do so by being inconspicuous (e.g. Dhondt & Schillemans 1983) or by being blatant (Myers *et al.* 1979, Davies & Houston 1981). In the visually disruptive habitat of the Snares Islands, snipe were difficult to detect at distances over 10 m from my eye level; from the ground, detection distances often would be much shorter. An intruder that did not call could avoid detection by the alpha male much of the time. Beta males called rarely (and gamma males never did) and so were inconspicuous. However, intruding beta and gamma males made no attempt to avoid alpha males, and sometimes fed alongside them.

Assuming that expulsion of intruders is costly in terms of time or energy (Myers *et al.* 1979, 1981, Davies & Houston 1981), high rates of intrusion may lead to the cessation of territory defence (see also Gibb 1956, Davies 1976). Expulsion of intruding subordinates by alpha male snipe may be futile, as other subordinates could simultaneously be present, undetected, within the territory. While territory ownership was a prerequisite for obtaining a mate, alpha males did not defend food resources within their territories. Alpha males guarded their mates during courtship and laying, and defended their territories against those intruders that attempted to claim territory ownership (i.e. by calling). Nonterritorial birds had no social constraints on where they established their home ranges, but could only breed when the resident alpha male stopped defending his territory - temporarily (while chick-rearing) or permanently.

Breeding site fidelity

Migration (or non-migration) is a factor that has received little attention in studies of breeding dispersal by waders, yet it undoubtedly affects return rates of adults and young. Oring & Lank (1984) explicitly ignored migratory dispersal in their review, as all the species that they discussed were migratory, breeding did not occur on the wintering grounds and "...the birds were capable of precise homing from wintering to breeding areas". Migratory birds are expected to have lower return rates due to a combination of: (1) migration-induced mortality, (2) increased opportunities to assess alternative breeding sites, (3) association with conspecifics from other populations while on the wintering grounds or on migration, leading to recruitment to a different breeding site, and (4) vagrancy due to navigational error (Baker 1978). All four factors are probably positively correlated with the distance travelled during migration, hence return rates should be negatively correlated with the distance between breeding and wintering areas. While there is no *a priori* reason to expect sexual differences in return rates to vary with migration distance (unless the sexes winter in different areas), interspecific comparisons of breeding site fidelity and natal philopatry could be affected greatly.

An appraisal of breeding site fidelity rates for sandpipers given by Oring & Lank (Table I, 1984) supports the contention that migration distance affects return rates. Using mean breeding site fidelity rates for each species, short distance migrants (Redshank, Willet *Catoptrophorus semipalmatus*, Long-billed Curlew, and Black-tailed Godwit *Limosa limosa*) had the highest return rates (70 - 74%, mean 72%), while long distance migrants (Semipalmated Sandpiper, Stilt Sandpiper, Red-necked Phalarope *Phalaropus lobatus*, and Grey Phalarope *P. fulicarius*) had the lowest return rates (4 - 50%, mean 31%) regardless of their social systems. Medium distance migrants (Spotted Sandpiper *Actitis macularia*, Western Sandpiper, Least Sandpiper *Calidris minutilla*, Temminck's Stint *C. temminckii*, Dunlin, and Ruff *Philomachus pugnax*) had intermediate return rates (34 - 76%, mean 57%).

A sedentary species, such as New Zealand Snipe, would not only avoid the detrimental effects of migration on return rates, but continuous residency at the breeding site would enhance familiarity with the territory and prevent take-over attempts in the territory-owner's absence. Breeding site fidelity rates for New Zealand Snipe (males 82%, females 88%) are considered equivalent to mean annual survival rates, as territory fidelity was so high (males 100% of birds that 'returned', females 89%; the six females that changed territories between seasons all moved to adjacent territories, ie. about 58 m). The much lower breeding site fidelity rates for migratory scolopacids (see above) must be due to higher mortality rates, plus an unknown percentage of birds that change breeding sites between seasons.

In many birds breeding site fidelity decreases following nesting failure (e.g. Richdale 1957, Darley *et al.* 1977, Harvey *et al.* 1979), including waders (Oring & Lank 1982, Redmond & Jenni 1982, Gratto *et al.* 1985, Thompson & Hale 1989). Only in the Dunlin, which has high breeding site fidelity, were return rates independent of breeding success in the previous year (Holmes 1966, Soikkeli 1967, 1970a & b).

Previous breeding success and experience did not affect breeding site fidelity, territory fidelity or mate fidelity in New Zealand Snipe. Failed breeders had very few opportunities to change mates or territories, as all available habitat was contained in contiguous territories and mortality rates of territory holders were so low (about 17% per annum). A breeding bird that chose to abandon its territory or mate (and therefore move location) would have had difficulty replacing it due to competition from the pool of nonbreeding birds (Baker 1978, Greenwood 1980). Some beta males may have even held a competitive advantage over an hypothetical alpha male that had left his territory: a prior resident (if present) always obtained a territory that was vacated. The reluctance of failed breeders to undergo breeding dispersal even though their breeding site or mate was possibly inadequate was not surprising as the costs of dispersal were high. The best option for a breeder with a low quality mate or territory may have been to stay on the territory until death of the mate or a neighbour permitted access to a new mate or a change in the territory boundaries.

Nonbreeding birds benefitted from occupying the same potential breeding site each year because prior residency was an important factor in the acquisition of a territory (see Greenwood 1980). Even within a breeding season, a nonterritorial bird that maintained a topographically fixed home range occasionally bred (as a beta male or female) whereas a transient bird (gamma male) never did. The most profitable strategy for a male unable to obtain a territory was to maintain a home range overlapping 2 - 3 territories, thus permitting a low chance of breeding that season (with a failed alpha female) and a high chance of acquiring one of the territories over the next 1 - 2 years.

Natal philopatry

New Zealand Snipe chicks return to the vicinity of their natal territory to breed. The return rate of snipe chicks (30% overall, and 46% of fledglings) was far higher than recorded for scolopacids elsewhere (1 - 11% for ten species; Oring & Lank 1984). In the only other study that has looked at the effect of prefledging mortality on the rates of return, Thompson & Hale (1989) recorded an overall return rate of 2.2% for Redshank chicks, but suggested that up to a third of fledglings return to breed near their birth site. Prefledging mortality for New Zealand Snipe (about 1.6% per day; Chapter 1) was much lower than for Redshank (13.2% per day for the first 20 days; data from Thompson & Hale 1989), presumably due to the effective absence of predators on the Snares Islands (see Chapter 1). The low levels of natal philopatry recorded for other waders are probably due mainly to higher mortality in their first year of life, although a proportion of birds would disperse to other breeding sites (e.g. Soikkeli 1967, 1970a & b, Hildén 1978).

As with most other monogamous scolopacids, New Zealand Snipe showed no sex bias among returning young (Soikkeli 1970a & b, Holmes 1971, Gratto *et al*. 1985, but see Redmond & Jenni 1982). However, there was a slight male bias in natal dispersal distances. Most young males established territories within two territory diameters of their natal territory after 1 - 2 years of maintaining a home range adjacent to their natal territory. Males chose where to live as beta males; there were no constraints on where a male established his home range. The location of a male's eventual territory was determined by the disappearance of alpha males within or adjacent to his home range during his first three years.

Most young female snipe were paired as one-year-olds, 3 - 4 territory diameters from their natal territory. The location of a female's territory was determined largely by the disappearance of alpha females from the study area during her first two years. The sex bias in natal dispersal distances was due to young males choosing to live near their natal territories, while young females moved to wherever there was an unpaired alpha male. Sex biased natal dispersal in New Zealand Snipe was driven by the presence of a pool of nonterritorial males, while there were relatively few nonterritorial females. The underlying cause of the male-biased sex ratio within the study area (range 0.50 - 0.96 females per male) was not determined, but it was present during the six years of this study.

The island environment

Stamps & Buechner (1985) concluded that as other ecological factors that might regulate density are relaxed or absent on islands, intraspecific regulative processes are probably more important than for mainland populations. Intraspecific competition (density) was positively correlated with mortality rates in New Zealand Snipe. Access to breeding opportunities for males and females was constrained by deaths of alpha males and females leaving vacancies to be filled. Thus, intraspecific competition in New Zealand Snipe not only determined what proportion of nonbreeders gained access to mates, but also the total number of nonbreeders able to enter the breeding population.

Chapter 4

Effects of the 1982-83 El Niño event on two endemic landbirds on the Snares Islands, New Zealand.

Emu (in press).

Abstract

The major El Niño/Southern Oscillation event of 1982-83 disrupted weather patterns at the Snares Islands in the New Zealand subantarctic. There was an abnormal preponderance of westerly and south-westerly winds, rainfall was 3.6 times greater than the mean for the succeeding four summers, and temperatures were significantly cooler than three of the four subsequent summers. Compared with four succeeding years, the few Snares Island Snipe *Coenocorypha aucklandica huegeli* that bred in 1982-83 did so 24 days later on average, breeding was successful in significantly fewer territories (20% cf. 46 - 84%) and 3.1 times fewer young per territory left nests (0.4 cf. 0.91 - 1.90). Adult mortality measured by density in the winter following the El Niño was 2.5 times greater than the mean for the 1984 to 1987 winters. High adult mortality and low recruitment of juveniles following the 1982-83 season resulted in a low density of snipe in the study area in 1983-84. Only one Black Tit *Petroica macrocephala dannefaerdi* nest was found in 1982-83. The first tit fledglings seen in 1982-83 were a full month later than the mean date for three subsequent years. Widespread reproductive failure and delayed breeding by Snares Island Snipe and Black Tit in 1982-83 and high mortality of adult snipe during the 1983 winter were probably caused by a reduction in their invertebrate food supply.

Introduction

El Niño is the name applied to the periodic appearance of anomalously warm surface water in the eastern Pacific Ocean. The El Niño Current is driven by a larger atmospheric phenomenon known as the Southern Oscillation (Philander 1983, Rasmusson & Wallace 1983). El Niño/Southern Oscillation (ENSO) episodes occur at irregular intervals of two to ten years, with a periodicity of about four years (Cane 1983). ENSOs in the eastern tropical Pacific are characterised by high sea-surface temperatures, high sea levels, depressed thermoclines and nutriclines, and greatly increased rainfall (Barber & Chavez 1986) and are typically accompanied by large reductions in plankton, fish and seabirds (Murphy 1936, Cushing 1982, Barber & Chavez 1983).

The ENSO event of 1982-83 was the strongest oceanographic disturbance in the eastern Pacific this century (Cane 1983, Rasmusson & Wallace 1983). Biological consequences of the 1982-83 ENSO included a 20-fold decrease in phytoplankton production in the eastern tropical Pacific, with drastic ecological consequences to higher trophic levels (Barber & Chavez 1983 & 1986, Grove 1984). Failure of food supply resulted in huge mortality and total reproductive failure of many seabird species along the Peruvian coast (Arntz 1984), on the Galapagos Islands (Gibbs *et al.* 1987, Robinson 1987, Valle & Coulter 1987) and on Christmas Island in the central Pacific Ocean (Schreiber & Schreiber 1984). Five age classes of Galapagos fur seal *Arctocephalus galapagoensis* were wiped out almost entirely, as was the youngest age class of Galapagos sealions *Zalophus californianus wollebaeki* (Trillmich & Limberger 1985).

The meteorological effects of the 1982-83 ENSO were felt throughout the Pacific Basin, and possibly as far afield as North America, the Indian subcontinent, Africa and Eurasia (Rasmusson & Wallace 1983, Glantz 1984, Gowan 1984, Rasmusson 1984, Ward 1985). During December 1982 to March 1983 New Zealand experienced frequent strong west and south-west winds, resulting in low temperatures over the whole country, floods in Otago, Southland, Nelson, Marlborough and the southern North Island, and severe drought in Canterbury, Gisborne and Hawkes Bay (New Zealand Meteorological Service 1982 & 1983, Gordon 1985, Ward 1985). Although the 1982-83 ENSO is known to have affected New Zealand weather patterns, there are no records of the biological consequences of the event in New Zealand. This paper outlines anomalies in the breeding seasons of two endemic landbirds: Snares Island Snipe *Coenocorypha aucklandica huegeli* and Black Tit *Petroica macrocephala dannefaerdi*, and associated weather conditions on the Snares Islands (48°02′S 166°36′E) in the New Zealand subantarctic during the 1982-83 ENSO.

Methods

Daily weather data were recorded on Station Point on the east coast of Main (North East) Island, Snares Islands Nature Reserve during six University of Canterbury expeditions: 2 December 1982 - 20 February 1983; 30 November 1983 - 29 February 1984; 26 November 1984 - 16 February 1985; 2 November 1985 - 10 March 1986; 22 October 1986 - 20 February 1987 and 7

November - 8 December 1987. Weather data summarised here are wind direction and dry bulb temperature at 0900 hrs (NZST), and total rainfall for the months December and January between 1982-83 and 1986-87.

Snares Island Snipe were studied intensively during all of the expeditions, with the exception of the period 30 November 1983 - 2 February 1984. The study area of *Olearia lyalli* forest north of Station Point held ten territories in 1982-83 and 1983-84, and was expanded to include 20 territories in subsequent years. All resident adults were individually colour-banded, and 45 nests were found within the 7.5 ha study area between 1982 and 1987. Seventy-three chicks of study pairs were captured. Ages of 38 were estimated by comparison of their measurements with measurements of the 35 chicks of known age (Appendix 2). First-egg laying dates for all 64 nests known to have been initiated by study pairs were recorded directly, or estimated from hatching dates (Chapter 1), egg weights (Chapter 2) or chick sizes. Density of resident adult snipe (breeders and nonbreeders) and between-season mortality were calculated each study season.

Casual observations of Black Tits were made each season, with the exception of November-December 1987, when they were studied intensively (McLean & Miskelly 1988). Information recorded in earlier years included the number of nests found, and the date when fledglings were first seen.

Results

The Snares Islands have a moist, cool temperate climate with predominantly west or south-west winds. During 1972 (the only year for which weather data are complete; Horning 1974) precipitation occurred on 301 days, although the total rainfall was only 1180 mm. By contrast, 930 mm of rain fell during the 80 days that the 1982-83 expedition was on the island. Rainfall during December 1982 and January 1983 was 3.6 times the mean rainfall for the same period in the following four years (Fig. 4.1a). The greatly increased rainfall in the summer of 1982-83 was associated with an even greater preponderance of westerly winds and with unusually cold temperatures. West or south-west winds occurred on significantly more days in December 1982 and January 1983 than in 1983-84 to 1986-87 (66% cf. 24 - 45%, $X^2_4 = 27.7$, $P < 0.0001$). In 1982-83 temperatures were not significantly lower than in 1983-84, but both

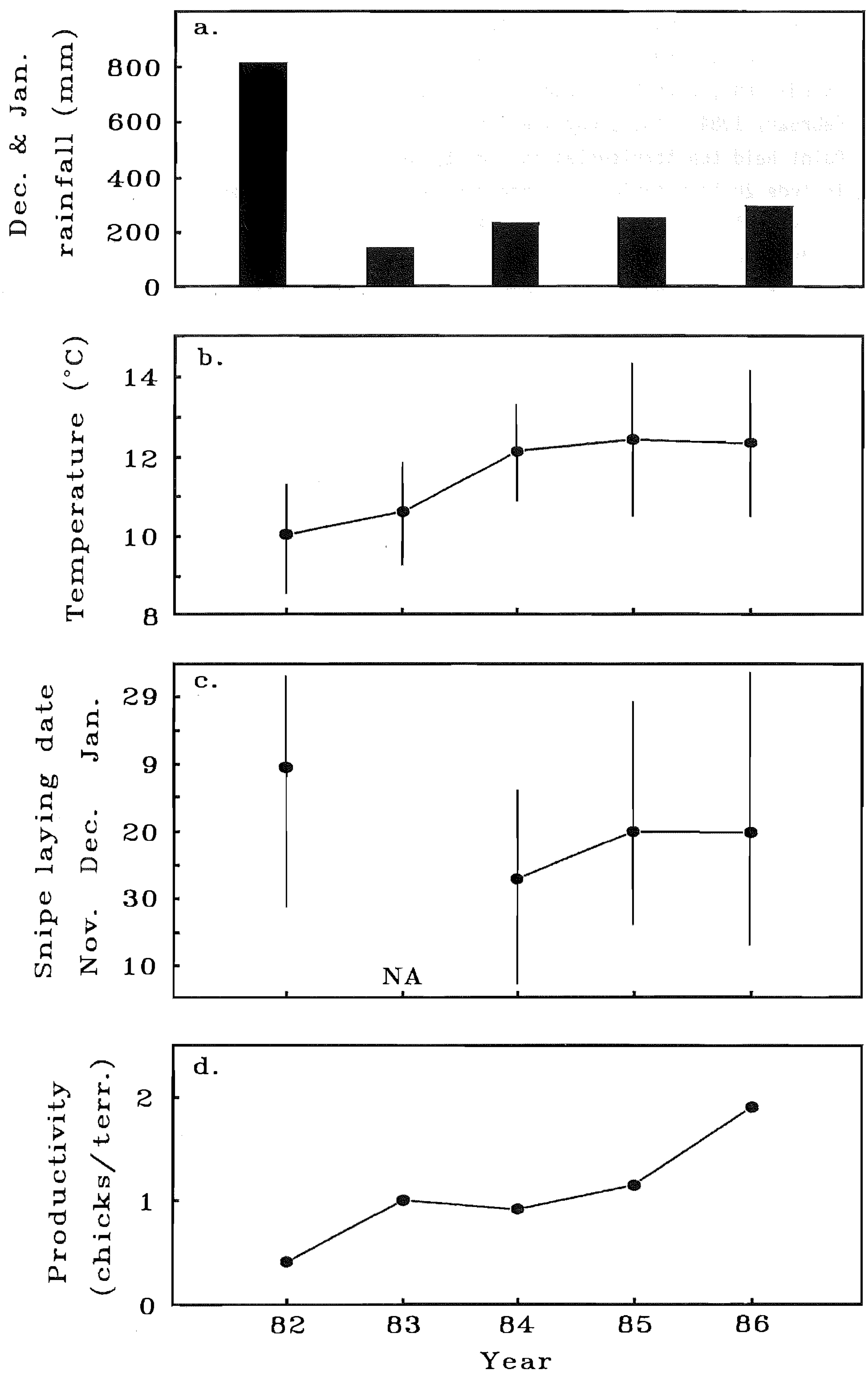
a.
Dec. & Jan. rainfall (mm)
0
200
400
600
800
b.
Temperature (°C)
8
10
12
14
c.
Snipe laying date
Nov. Dec. Jan.
10
30
20
9
29
NA
d.
Productivity (chicks/terr.)
0
1
2
82
83
84
85
86
Year

Figure 4.1. Weather conditions and snipe breeding parameters on the Snares Islands, 1982-83 to 1986-87.
a. Total rainfall for December and January.
b. Dry bulb temperature at 0900 hrs, December and January. Vertical bars are one standard deviation.
c. Mean and range of laying dates for first breeding attempts by snipe. No data were available for 1983-84.
d. Minimum number of snipe chicks hatched out per territory.
Snipe bred late and produced few chicks during the 1982-83 ENSO.

1982-83 and 1983-84 were significantly colder than the following three years ($F = 28.2$, $P < 0.05$; Fig. 4.1b).

Only four breeding attempts were recorded in the ten snipe territories in 1982-83, and only two pairs completed incubation. The mean first-egg laying date for the four females was 8 January, compared with a mean of 15 December for first-egg laying dates of first nests in three subsequent breeding seasons (Fig. 4.1c). The 20% of pairs that successfully hatched clutches in 1982-83 was significantly less than the 46 - 84% in the following four seasons ($X^2_4 = 13.0$, $P = 0.01$). The two broods of young were five and 18 days old when I left the island, but at least one chick from each brood survived to age one year. As dependent young were always present at the end of each study season, the best between season productivity estimate available was the minimum number of chicks per territory that left nests each year. The number of young that left nests in 1982-83 was 0.4 chicks/territory, compared with 0.91 - 1.90 chicks/territory in subsequent years (Fig. 4.1d).

Overall density of adult snipe in February 1984 was the lowest recorded in the six years (Fig. 4.2). Low snipe density in 1983-84 was due to a combination of low productivity in 1982-83 and high adult mortality during the 1983 winter. Snipe mortality on the Snares Islands is density dependent (Chapter 3), but adult mortality in relation to density following the 1982-83 season was 2.5 times higher than the mean for the following four winters (Fig. 4.3).

Only one Black Tit nest was found in 1982-83, compared with 11 to 37 nests in subsequent years. Tit nests are easy to locate on the Snares (McLean & Miskelly 1988), so the absence of nests in 1982-83 was likely to have been due to widespread reproductive failure, rather than observer

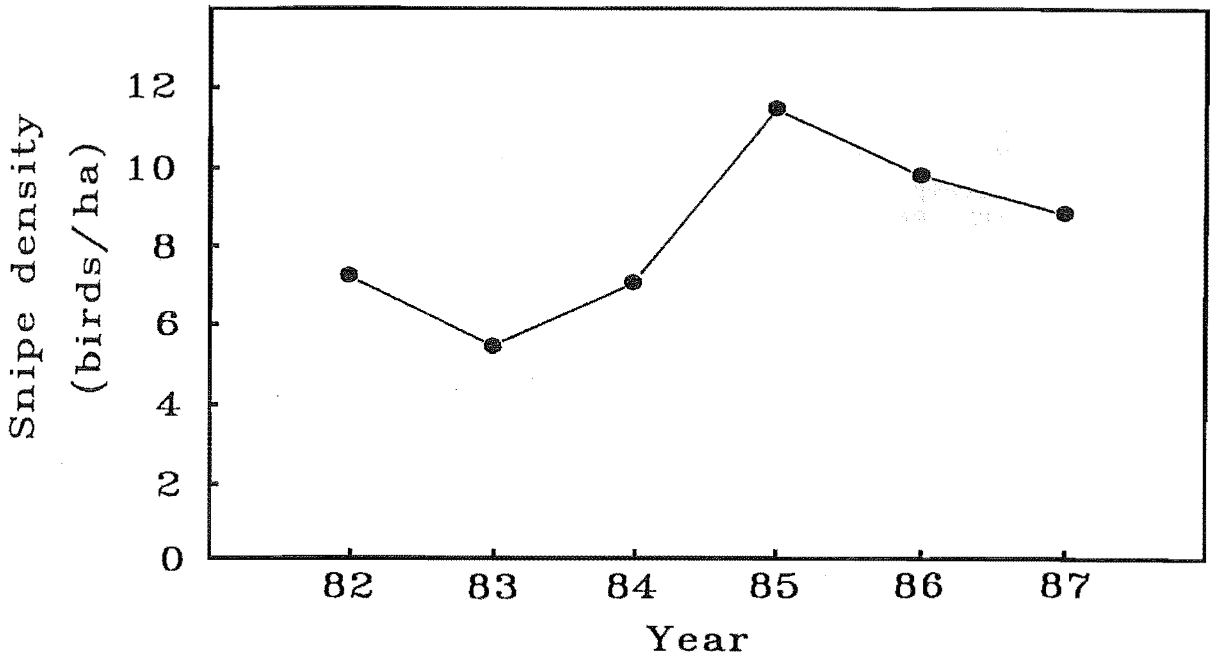

Figure 4.2. Density of adult snipe (breeders and non-breeders) in the study area, 1982-83 to 1987-88. Density reached a low of 5.4 birds/ha in 1983-84, the year following the 1982-83 ENSO.

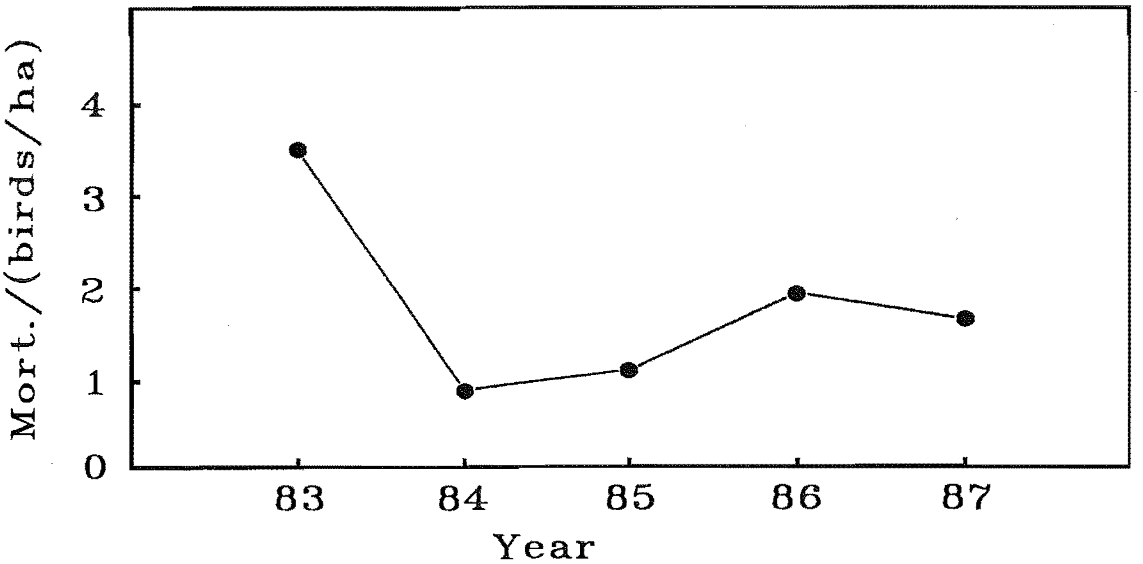

Figure 4.3. Winter mortality of adult snipe in relation to density, 1983 to 1987. Mortality was highest in the winter directly after the 1982-83 ENSO.

inexperience. The first tit fledglings found in 1982-83 were seen on 4 January, compared with a mean of 4 December for three subsequent seasons (range 1 - 6 December; McLean & Miskelly 1988).

Discussion

The high rainfall and low temperatures recorded on the Snares Islands in December 1982 and January 1983 were comparable with conditions recorded in southern and western areas of the South Island during the 1982-83 ENSO (New Zealand Meteorological Service 1982 & 1983, Gordon 1985, Ward 1985). Although Snares Island Snipe and Black Tit bred late and had poor breeding seasons during the 1982-83 ENSO, the processes by which their breeding seasons were disrupted are unclear.

Snares Island Snipe obtain all their food by probing in the soil column. A wide variety of prey is taken; important items include earthworms, amphipods, adult and larval Coleoptera, and dipteran larvae (Appendix 5). Densities of soil-dwelling invertebrates on the Snares Islands were not measured systematically in 1982-83, but subsequent work has shown that snipe breed later in seasons of low prey abundance (Chapter 5). Soil moisture and temperature are known to have a strong influence on earthworm activity and vertical distribution in the soil. When conditions near the surface become suboptimal, earthworms respond by either migrating deeper in the soil or entering a state of aestivation (Guild 1948, Reynolds & Jordan 1975, Edwards & Lofty 1977), and hence would be less available for foraging snipe. Potential effects of adverse weather conditions on other snipe prey are not known, however, at least two important snipe prey items (the large, conspicuous beetles *Prodontria* and *Hadramphus*) were much scarcer in 1982-83 than in subsequent years (pers. obs.). Low prey abundance following the 1982-83 ENSO may also have been responsible for increased mortality of adult snipe during the 1983 winter. Extended periods of cold weather are known to cause increased breeding failure and adult mortality in the closely related American Woodcock *Scolopax minor* (Rabe *et al*. 1983b).

Black Tits obtain most of their prey by gleaning on and within two metres of the ground (Best 1975). Their diet has not been studied in detail, but includes adult and larval Diptera and Lepidoptera (Stead 1948, pers. obs.). No attempt has been made to study food availability for Black Tits.

The poor breeding season of snipe and tits in 1982-83 was thought to be due to potential breeders not attempting to breed, rather than failure (eg. flooding) during incubation. Nest-building behaviour and feeding of incubating female tits by males are very conspicuous (McLean & Miskelly 1988) and would not have been over-looked. Snipe were studied so intensively in 1982-83 that the absence of a member of any pair in order to incubate would have been detected, even if the nest was not found. Although total rainfall was high in 1982-83, extensive flooding of Sooty Shearwater *Puffinus griseus* and Diving Petrel *Pelecanoides urinatrix* burrows was not observed. Burrows of these petrel species are prone to flooding during periods of heavy rain (e.g. in late January 1987; pers. obs.). None of the snipe nests that I have studied, including eight in late January 1987, has failed due to flooding (Chapter 1).

The poor breeding seasons of Snares Island Snipe and Black Tit in 1982-83 contrast dramatically with the greatly increased reproductive success of landbirds on the Galapagos Islands during the 1982-83 ENSO. The exceptionally high rainfall on the arid Galapagos Islands during the El Niño led to unprecedented plant growth and seed production (Gibbs & Grant 1987, Gibbs *et al.* 1987) and a greatly increased food supply for the landbirds (Gibbs & Grant 1987). Medium Ground Finch *Geospiza fortis*, Cactus Finch *G. scandens*, Large Cactus Finch *G. conirostris* and Galapagos Mockingbird *Nesomimus parvalus* bred repeatedly and increased greatly in numbers in 1982-83 (Curry 1985, Grant & Grant 1985, Gibbs & Grant 1987). Increased precipitation on the perpetually moist Snares Islands during the 1982-83 ENSO did not noticeably influence plant production. I suggest that the high rainfall and low temperatures on the Snares Islands inhibited invertebrate growth and reproduction directly by physical and/or physiological processes such as lowering metabolic rates, waterlogging the soil, and impairing movement and feeding.

Snares Island Snipe and Black Tit occur at high densities on the Snares Islands (McLean & Miskelly 1988; Chapter 3). Neither species invested much energy in reproduction during the 1982-83 ENSO compared with subsequent years. Between-year variation in reproductive investment is well known for the Kakapo *Strigops habroptilus* (Merton *et al.* 1984) but may be a widespread phenomenon in *K*-selected endemic New Zealand landbirds. I suggest that other ecologists conducting long-term studies in the South Pacific check their records for anomalies that may be linked to the major ENSO that occurred during the 1982-83 summer.

Chapter 5

Food availability and the timing of breeding by New Zealand Snipe.

Abstract

The effects of food availability and weather conditions on the timing of breeding by New Zealand Snipe *Coenocorypha aucklandica* were studied during two breeding seasons, and the start of a third, on the Snares Islands. Food availability was measured in three-week intervals by sampling the abundance and energy content of soil invertebrates (kJ/m^2), and by measuring the 'cost' of probing in the soil (kJ/m^2) with a penetrometer. The composite variable 'food availability' (kJ/m^2) was determined almost entirely by food abundance, as the cost of probing was minimal. Rainfall and air temperature fluctuated little within and between seasons, and these variations had little effect on food availability in most habitats. Food availability was lowest early in the breeding season, peaked in mid to late December, and remained relatively high through January and February. Body-weights of snipe in November were highly correlated with food availability. When food was more plentiful, females reached threshold laying weight sooner, and laid earlier. In both years, the first eggs to hatch did so during the initial peak in food availability. Food availability during the period that chicks were reared was significantly higher than during the pre-chick period. These results support both Lack's (1968) hypothesis that birds should raise their young when food is most abundant, and Perrin's (1970) hypothesis that the date at which each female lays is related to the food supply at the time of laying.

Introduction

The relationship of breeding schedule to food supply has been a central theme in avian breeding ecology since the pioneer works of Rowan (1926) and Baker (1938) established the link between the timing of breeding and annual peaks in food abundance. David Lack (1954, 1966, 1968) reviewed this relationship for all the major bird orders, and formulated what is now referred to as 'Lack's hypothesis': birds should raise young when food is most abundant, so that they "...produce, on average, the greatest possible number of surviving young". Lack based his hypothesis on the premise that food limitation was greatest during the time of maximum food demand, i.e. during brood-rearing. However, he also recognised (1968) that in environments with low food availability, females may be limited by food supply during egg formation. Thus, the breeding season may be limited by food supply either proximately (egg formation) or ultimately (selection for production of young when food is most abundant).

Perrins (1970) developed the idea that birds should breed as early as possible, based on the observation that early breeders raised more young than late breeders (e.g. Perrins 1965, 1966, Harris 1969, Caccamise 1978, Finney & Cooke 1978, Slagsvold 1982, Murphy 1986). If there is selection for early breeding, all females would be constrained by nutrient availability during egg formation (Perrins 1970, Martin 1987). Many studies have shown that when food supply is increased naturally or artificially, birds lay earlier (see reviews in Martin 1987, Arcese & Smith 1988). Obviously, there could be a trade-off between the energy requirements of the female during oogenesis, and the energy requirements of developing chicks, as the two events are separated by three to over eleven weeks, depending on the species (Perrins 1970).

A major problem in studies of food supply and breeding is the difficulty in measuring food availability from the birds' perspective. Most workers in this field have used indices of prey abundance based on techniques such as litter sampling, visual counts of flying or flushed insects, sweep-netting, assessing caterpillar frass-fall, malaise traps, sticky traps, the formalin method for earthworms, soil core sampling and pitfall trapping (e.g. Högstedt 1974, Greenlaw 1978, Maxson & Oring 1980, Blancher & Robertson 1987, Green 1988). These techniques may bear little relationship to the difficulty birds have in capturing prey. In this study of food availability and the breeding schedule of New Zealand Snipe *Coenocorypha aucklandica* I devised a sampling procedure that allowed both food abundance and an estimate of the cost of capture to be measured in the same units (kJ/m^2). The composite variable 'Food availability' (also in kJ/m^2) was considered a more realistic estimate of prey availability than estimates based simply on prey abundance.

New Zealand Snipe occurred at high densities on the Snares Islands (up to 11.5 birds/ha) and many birds were unable to obtain territories or mates (Chapter 3). I argue elsewhere (Chapter 1) that the breeding system of New Zealand Snipe has been constrained through intense intraspecific competition for food in a stable environment. Most New Zealand Snipe were monogamous. Males courtship-fed females for the three weeks preceeding laying. Two large eggs were laid three days apart; incubation began when the second egg was laid, was shared equally by the sexes, and took 22 days (Chapter 1, Appendix 2). The brood was split on hatching; the male cared for the first chick to leave the nest and the female cared for the remaining chick. Chicks were fed by adults until at least 41 days old, and reached independence at c.65 days (Chapter 1). Adults that lost their dependent chick (or never had one) often renested with their previous mate (43%); if their first mate was still caring for a chick, birds of either sex occasionally nested with a new mate (14% of emancipated males, 25% of emancipated females). Reproductive output was constrained by the small clutch size, the high level of parental investment by both sexes, the long period of chick dependence, and the limited opportunities for acquiring additional mates (Chapters 1 & 2). The low per pair production of young (Chapter 1) and density-dependent mortality during the nonbreeding season (Chapter 3) indicated that New Zealand Snipe were constrained by food availability throughout the year.

In this study, I investigate the relationship between food availability, weather conditions, and breeding by New Zealand Snipe. Factors considered include breeding condition (body-weights of females and males), commencement of laying, cessation of laying, hatching dates, chick-rearing and chick mortality.

Study area and methods

Study area

The relationship between food availability and the timing of breeding by New Zealand Snipe was studied during two breeding seasons, and the start of a third, on the Snares Islands, south of New Zealand. The Snares Islands (48°02'S 166°36'E) are a small, uninhabited group of islands that have remained relatively unmodified by humans. The plant cover of the islands is comparatively simple in structure and composition, with one tree species and two tussock grass species covering most of the two largest islands (Fineran 1964, 1969). The study area used for snipe research was 7.5 ha of predominantly *Olearia lyalli* forest, lying between Boat Harbour and Punui Bay on the east coast of Main Island (Horning 1978). Fieldwork was carried out during the periods 2 November 1985 to 10 March 1986, 22 October 1986 to 20 February 1987, and 7 November to 8 December 1987.

The study area was selected for ease of access from the Biological Station, and for its high density of snipe (Chapter 3). Snipe on the Snares Islands were most numerous in areas with diverse ground cover, such as occurred under the margins of *Olearia* and *Brachyglottis* forest on the low-lying eastern side of Main Island (unpubl. data). The entire study area was marked out in a 20 m grid. The area of different ground covers within each 20 x 20 m grid square was estimated to the nearest 5% (20 m^2) during 1985-86 and 1986-87. The mean percentage areas of ground covers within the study area were: Bare peat 32%, Tussock (mainly *Poa tennantiana*) 29%, Fern (mainly *Polystichum vestitum*) 13%, swards of *Callitriche* and *Crassula* 10%, bare rock 6%, Mud 5%, Punui *Stilbocarpa robusta* 2%, Penguin colony 2%, and open water 2%. Snipe used all habitats except bare rock and open water, but concentrated feeding activity in Tussock, Fern and *Callitriche* (unpubl. data).

Snipe

The study area contained about 20 snipe territories. All 45 - 64 adult snipe resident in the study area were individually colour-banded (total = 78). Adult snipe were recaptured regularly to monitor body-weights and record brood-patch, cloaca and moult condition. Most adults were hand-netted at night with the aid of a spot-light, but birds of particular interest (e.g. females that had not laid) were stalked and hand-netted during the day. Body-weights were recorded to 0.5 g; 12 - 25 (mean = 17) adult males and 10 - 24 (mean = 15) adult females were weighed during each of the 13 three-week sampling periods.

Pairs were identified by prolonged consorting, courtship feeding, mating or attendance at the same nest, observed during daily surveys of the study area. Laying dates for all 45 breeding attempts in 1985-86 and 1986-87, plus five in November 1987, were determined by observations of pair behaviour plus body-weight changes (n = 5), watching nests during laying (n = 7), back-calculating from rates of egg weight-loss (n = 6; Chapter 2), or back-calculating from hatching dates (n = 32). Hatching dates were observed directly (n = 28) or back-calculated from chick measurements (n = 13; Appendix 2). The date that laying started each year was estimated by calculating the mean (and range) of first-egg laying dates for the first five females to lay in the study area each year, as only five laying dates were available for the 1987-88 season.

Chicks were captured and banded in the nest (n = 22) or when first sighted away from the nest (n = 22). Chicks were recaptured by hand-netting whenever encountered during daytime surveys, or when I was searching for adults at night. A chick was assumed to have died if its parent was seen three or more times unaccompanied by the chick, and the chick was not seen subsequently. The date of death was taken to be the day that the chick was last seen. Live chicks were seen, on average, every 3.6 days (Chapter 1).

Food availability

Snipe captured all their prey by probing (Miskelly 1984). A wide variety of soil invertebrates was eaten; frequently consumed items included earthworms, terrestrial amphipods, adult and larval Coleoptera, and larval Diptera. All of the more abundant taxa of soil invertebrates on the Snares Islands (with the exception of adults of the large carabid *Mecodema*) have been identified in snipe faeces (Appendix 5) or have been seen to be eaten by snipe.

Food abundance for snipe was estimated by systematic sampling of soil invertebrates. At 7-day intervals, I collected a soil sample from each of the following habitats: Tussock, Fern, Punui, *Callitriche/Crassula* (referred to as *Callitriche* for the remainder of this paper), Bare peat, Penguin colony, and Mud. Samples were taken from the nearest patch of the chosen ground cover to a randomly chosen grid marker within the study area (i.e. seven different grid markers were chosen each week). Punui was rare in the study area in November 1987, and so this habitat was not sampled that month. Samples were collected for 18 weeks in each of 1985-86 and 1986-87, and four weeks in November 1987 (total = 276 samples). Wherever possible, samples were collected on the same calendar day each year.

Each soil sample had a surface area of 0.05 m^2 (22.4 x 22.4 cm) and was dug with a spade to c.6 cm depth (the maximum length of a snipe's bill). Samples were sealed in plastic bags until they were sieved later the same day. Drier samples were broken up and passed through a 3.5 mm mesh sieve; most plant material and stones were removed at this stage, along with larger invertebrates (e.g. *Eodrilus* earthworms, adult *Prodontria* beetles, final instar *Prodontria* larvae). The remaining siftings were spread on white sorting trays to a depth of 5 mm (7 - 12 trays per sample), then moistened with sea water. All invertebrates that moved or showed themselves were collected; trays (5 at a time) were watched closely for a minimum of 15 min, or for 10 min from the time that the last invertebrate was collected. Water-saturated soil samples (Mud and, often, Penguin colony) were broken up in a bucket of fresh water, then washed through 3.5 and 0.5 mm mesh sieves. Material retained in each sieve was carefully searched for invertebrates. All invertebrates larger than mites, Collembola and nematodes were collected. Extraction efficiency was not measured, but the technique was extremely thorough; the seven samples usually took 1.5 - 2 days to collect and process. Invertebrates collected (n = 21 255) were stored in 70% ethanol and returned to Christchurch for analysis. In addition, representative samples of all major taxonomic groups of soil invertebrates were collected in early March 1986 and kept frozen until analysed.

Each sample of invertebrates was sorted by taxa under a binocular microscope (most to species level and life-history stage), counted, and oven-dried to constant weight at 60°C. After drying, each taxon was weighed to 0.001 g on a Salter electronic balance, samples were then pooled by taxon until sufficient material was obtained (minimum of 0.4 g dry weight) for combustion in a Gallenkamp bomb calorimeter. Large and/or numerous taxa provided sufficient material for up to 17 firings per year (Table 5.1), but small or rare taxa had to be pooled across years and/or across related taxa (Table 5.1).

Calorimetry values (kJ/g dry weight) from the frozen invertebrates were used to correct for changes in energy content due to ethanol storage. Corrected energy content values for each taxon, or taxon/year, are given in Table 5.1.

Mean energy content (kJ/g dry weight) for each taxon or taxon/year was multiplied by the dry weight of each taxon from each sample to yield (by summation) the energy content (kJ/m^2) for each soil sample. This figure is referred to as 'Food abundance' for the remainder of this paper. Mean food abundance (kJ/m^2) for each three-week sampling period was calculated by weighting the energy content for each habitat by the total area of that habitat (m^2) in the study area. Thus, each three-week estimate of food abundance was based on 21 (or 18) samples from seven (or six) habitats.

As snipe obtained all their food by probing, the cost of food extraction was estimated by measuring soil penetrability with a Soiltest Pocket Penetrometer (Model CL-700, with CL-701 adaptor for very soft samples). Ten readings of soil penetrability (kg/m^2) were taken at each of the 276 soil sample sites. As the penetrometer reading is equivalent to the pressure required to penetrate the soil, the force that a snipe would have to exert to probe the soil is the penetrometer reading x the cross-sectional area of the snipe's bill. Work (energy) equals force x distance, therefore the energy (J; 1 J = 1 kgm) required for a snipe to

Table 5.1. Energy content of representative snipe prey items collected in the study area.

Soil invertebrates	Energy content (kJ/g dry weight) n	Mean	s.d.
Annelida			
Hirudinea			
Ornithobdella	1	28.1	-
Oligochaeta			
Megascolecidae			
Eodrilus (1985-86)	17	24.3	1.7
(1986-87)	10	23.3	1.1
(Nov. 1987)	4	22.5	0.6
Megascolecidae spp. (1985-86)	12	27.4	1.3
(1986-87)	5	25.8	2.2
(Nov. 1987)	1	25.5	-
Megascolecidae egg cocoon	4	22.4	1.1
Enchytraeidae	2	23.9	0.7
Crustacea			
Amphipoda (1985-86)	9	24.1	1.7
(1986-87)	5	26.0	1.8
(Nov. 1987)	2	30.5	3.1
Isopoda	1	29.6	-
Araneae, Opiliones, Acari	1	29.6	-
Myriapoda, Symphyla, Chilopoda	2	28.3	1.9
Orthoptera eggs	2	23.7	0.2
Coleoptera			
Carabidae adults	6	32.7	2.0
larvae & pupae	5	32.0	2.2
Scarabaeidae			
Prodontria adults (1985-86)	8	26.5	2.4
(1986-87)	2	26.3	2.4
(Nov. 1987)	2	34.5	0.7
larvae (1985-86)	10	34.2	2.0
(1986-87)	10	36.5	2.9
(Nov. 1987)	3	31.8	0.2
Curculionidae adults	5	28.9	4.9
larvae & pupae	2	30.4	0.8
other Coleoptera adults	4	28.3	2.5
larvae & pupae	1	27.9	-
Diptera			
Tipulidae larvae & pupae	2	26.6	2.8
Syrphidae larvae & pupae	1	26.0	-
other Diptera larvae & pupae	1	27.9	-
Lepidoptera larvae and pupae	1	28.1	-

probe in soil with penetrability P is given by:

$$E = \frac{P \times A \times D}{100}$$

where E = energy (J), A = cross-sectional area of the bill (c.0.2 cm^2), and D = the depth probed (taken as 3 cm, half the bill length).

Snipe captured prey using a combination of exploratory and pursuit probing, as described by Rabe *et al.* (1983a) for American Woodcock *Scolopax minor*. I was not able to estimate by observation prey capture rates in relation to prey density. To estimate the energetic cost of probing by snipe, I required an estimate of the number of probes per unit area required to locate all the prey present. Snipe probably locate prey using a combination of tactile information and chemoreception (Tuck 1972, Burton 1974, van Heezik *et al.* 1983, Gerritson *et al.* 1983, Gerritson & Meiboom 1986). Assuming that snipe were able to detect all prey within a radius r of the bill-tip, the most efficient spacing of probe holes for maximal coverage of an area of soil would have been close hexagonal packing of probe holes $2r$ apart. Measurement of minimum distances between snipe probe holes in areas of densely probed mud and soft soil indicated a 'sensory distance' (r) of 0.43 cm, and a 'sensory area' of 0.57 cm^2; therefore, c.17 540 probes would be required to systematically search 1 m^2 of soil. Assuming that r was constant between habitats, the cost of extraction (kJ/m^2) for each habitat was determined by multiplying P by 0.105 (i.e. $A \times D \times 0.1754$).

Food availability (or Net energy) in kJ/m^2 for each soil sample was calculated by subtracting 'Cost of extraction' from 'Food abundance'. Although I have used the term 'Net energy' in place of 'Food availability' to save space in figures and tables, the term 'Net energy' refers only to the total energy content of soil invertebrates/m^2 minus the energy required to probe intensively 1 m^2, given the above assumptions. No attempt was made to estimate capture efficiency, assimilation efficiency, locomotory costs or energy budgets for foraging snipe.

Weather

Daily weather records were taken within the study area (at Station Point). Information used in this paper are total rainfall (mm) and the mean air temperature (½[max + min]) during the five days preceeding each soil sampling day.

Seasonal changes in soil invertebrate abundance are likely to be ultimately driven by seasonal changes in meteorological conditions (particularly temperature, photoperiod and precipitation), although these may act proximately through their effects on plant growth. The climate of the Snares Islands is remarkably aseasonal for a temperate land mass. Mean monthly air temperature in 1972 (the only year for which complete records are available; New Zealand Meteorological Service 1972) ranged between 6.9°C in June and 13.5°C in February, with a mean of 9.8 ± 2.1°C. Rainfall occurred evenly throughout the year, with monthly totals varying between 47 and 220 mm (mean 123 ± 51 mm). The periods when soil invertebrates were sampled in this study included the warmest months of the year (late summer), and so were likely to include annual peaks in prey abundance.

Measurements are given as mean ± s.d. unless otherwise stated.

Results

Temporal patterns in food availability

Effects of weather conditions

Food availability (food abundance minus cost of extraction) was controlled almost entirely by food abundance, as the cost of extraction (kJ/m^2) averaged less than 0.1% of food abundance (kJ/m^2; Table 5.2). Soil penetrability (and hence cost of extraction) is determined by soil particle size, compaction, water content and the presence of living or dead organic matter, especially plant rootlets. The Snares Islands are blanketed by a thick layer of peat, the surface layers of which are moist and soft due to the combined effects of the frequent (though light) rainfall and the burrowing activity of abundant seabirds (Fleming *et al*. 1953, Warham & Wilson 1982). Cost of extraction varied four-fold between the habitats surveyed (Table 5.2) but was not tightly correlated with total rainfall over the previous five days (r^2_{37} = 0.0001 - 0.079). Two habitats did show a significant negative correlation between rainfall and the cost of extraction (Tussock and Penguin colony; Table 5.2) and there was an overall effect of rainfall on the mean cost of extraction when all seven habitats were combined (P = 0.02; Table 5.2). Cost of extraction exceeded food abundance for 33 samples (15 from Mud, 15 from

Penguin colony, and three from Bare peat) where the number and size of prey items collected were small. The ground surface in the study area was never seen to be cracked or dusty, and so it is unlikely that soil penetrability limited snipe feeding during this study.

Table 5.2. The effect of increasing rainfall on food abundance, cost of extraction and food availability (= food abundance minus cost of extraction), and the effect of increasing mean air temperature on food availability for New Zealand Snipe. Energy values (kJ/m^2) are the means for each habitat, based on 36 samples from Punui, and 40 samples from the remaining six habitats.

		Rainfall			Rainfall			Rainfall			Temperature	
		Food abundance			Cost of extraction			Food availability				
Habitat	df	kJ/m^2	r	P	kJ/m^2	r	P	kJ/m^2	r	P	r	P
Tussock	37	454.3	0.24	0.12	0.20	-0.28	0.05	454.1	0.24	0.12	0.04	0.93
Fern	37	183.0	-0.04	0.95	0.15	0.03	0.97	182.9	-0.04	0.95	-0.06	0.87
Punui	34	293.6	0.08	0.78	0.13	-0.24	0.14	293.5	0.08	0.78	0.21	0.25
<u>Callitriche</u>	37	219.2	-0.05	0.91	0.17	-0.05	0.92	219.1	-0.05	0.91	0.05	0.93
Bare peat	37	91.4	0.16	0.36	0.16	-0.18	0.32	91.2	0.17	0.36	0.26	0.10
Penguin colony	37	11.0	-0.24	0.12	0.11	-0.35	0.01	10.9	-0.24	0.12	0.06	0.88
Mud	37	14.3	-0.34	0.01	0.05	-0.24	0.12	14.3	-0.34	0.02	-0.02	0.99
Unweighted mean	37	179.5	0.18	0.30	0.14	-0.33	0.02	179.4	0.18	0.30	0.20	0.25

Food abundance varied 41-fold between habitats, and was highest under plants (Table 5.2). Rainfall during the 1985-86 and 1986-87 summers had little effect on food abundance (Table 5.2). In only Mud did rainfall have a significant effect on both food abundance and food availability. As the water content in Mud increased, food abundance declined (r^2_{37} = 0.11, P = 0.015).

Air temperature from November to February also had little effect on food availability within seasons (Table 5.2). Rainfall and air temperature were not correlated (r_{35} = 0.10, P = 0.70), and they did not have a synergistic effect on food availability, although they did affect the mean cost of extraction (r_{34} = 0.45, P = 0.01).

Differences in food availability and weather conditions between years

There was little overall difference in food availability and weather conditions between 1985-86 and 1986-87. Data were collected from 7 November to 20 February in both years; during these periods, food availability averaged 199.6 kJ/m^2 in 1985-86 and 276.2 kJ/m^2 in 1986-87 (t_{30} = 1.31, P = 0.20; Fig. 5.1). Rainfall averaged 17.2 mm per five-day interval in 1985-86 and 24.1 mm in 1986-87 (t_{30} = 0.96, P = 0.35); mean daily air temperature was 12.2°C in both years. Both years were significantly warmer and drier than 1982-83, when increased rainfall and low temperatures were thought to have reduced food abundance (Chapter 4).

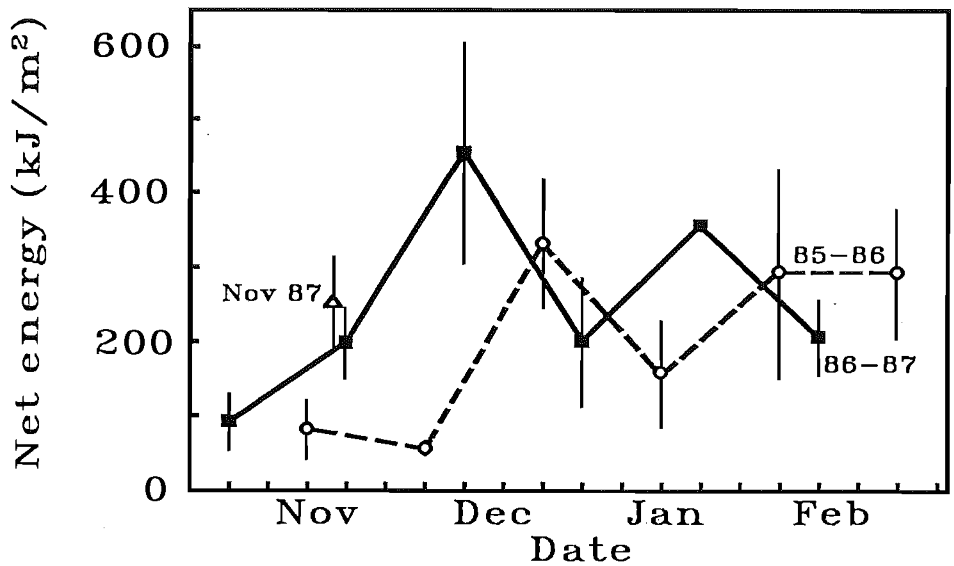

Figure 5.1. Variation in mean food availability in the study area during the 1985-86 and 1986-87 snipe breeding seasons, and in November 1987. Error bars represent one standard deviation of the mean.

Although mean food availability did not vary between 1985-86 and 1986-87, there were differences in when minima and maxima occurred (Fig. 5.1). Food availability peaked earlier in 1986-87, but declined during February. The 1985-86 peak occurred slightly later, but food availability remained at a similar level until at least the end of February (Fig. 5.1).

Three years of data on food availability and weather conditions at the start of the snipe breeding season (November) were collected (Fig 5.1

and Table 5.3). Food availability in November varied significantly between years ($F_{2,9}$ = 4.30, P = 0.049) and appeared to be positively correlated with temperature, and negatively correlated with rainfall (Table 5.3), although the sample size (three) was too small for statistical analysis.

Table 5.3. Mean daily rainfall, mean daily air temperature and mean food availability in the study area during November 1985, 1986 and 1987.

	Year		
	1985	1986	1987
Rainfall (mm)	4.2	3.1	0.5
Temperature (°C)	9.9	10.6	11.4
Net energy (kJ/m^2)	78.9	189.1	258.1

Variation in female snipe body-weight in relation to the breeding cycle

A clutch of two eggs represented about 42% of mean female body-weight in New Zealand Snipe (Chapter 1). Before laying, female snipe reached a threshold body-weight of about 142 g (Fig. 5.2), which was about 28 g heavier than the mean body-weight of non-laying females. Most of this weight gain was achieved in the three weeks before laying (Fig. 5.2), which corresponded to the period when females were courtship-fed by males, and when copulation occurred (Chapter 1).

Seven paired females did not lay during the two years of intensive study. None of these birds was recorded as weighing over 122 g (mean maximum body-weight 116.1 ± 5.0 g, range 108 - 122g).

Most females were able to recover rapidly from the stress of laying, as the mean body-weight of incubating females (121.6 ± 5.4g, range 116.2 - 127g, n = 37) exceeded the mean body-weight of non-laying paired and unpaired females (113.7 ± 3.9 g, range 109.8 - 117.6 g, n = 26; Fig. 5.2). Successful female breeders rearing a chick had a mean body-weight of 111.4 g, significantly less than the mean body-weight of females that had lost their chick (119.3 g, see Fig. 5.2 and Chapter 1).

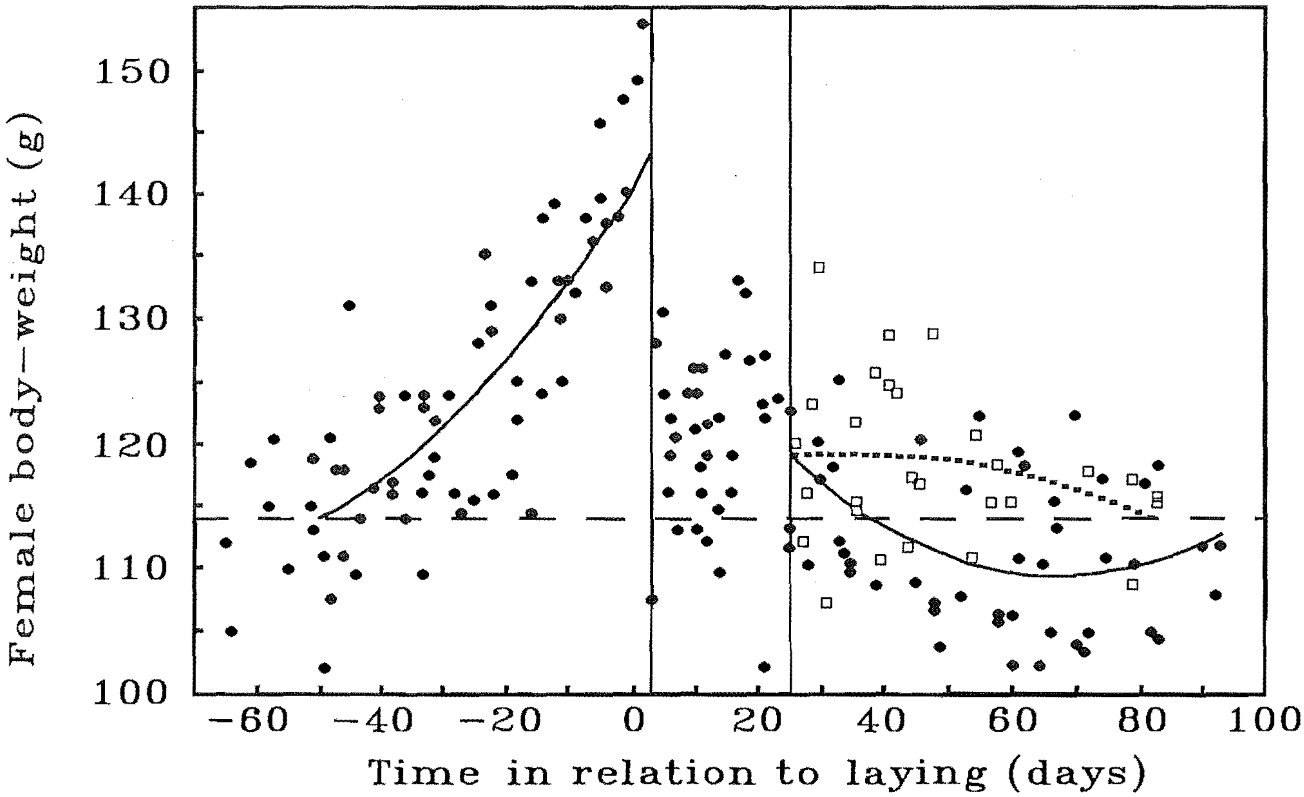

Figure 5.2. Variation in female snipe body-weight in relation to the date of laying of the first egg in a clutch (day 0). Vertical lines mark the beginning and end of incubation (days 3 and 25 respectively). The horizontal dashed line represents the mean body-weight of females that did not lay (both paired and unpaired females). Open squares and dotted line = failed breeders (clutch deserted, the female never had a dependent chick due to one egg failing to hatch, or the female's dependent chick died); date of failure was set to day 25 for all failed breeders. Sample points based on 274 weighings of 49 different females (1 - 16 per bird). Curves were fitted using the Maximum Likelihood Program (Ross 1980).

Food availability and snipe body-weights

Food availability at the start of the breeding season had a significant effect on body-weights of both female and male snipe. Female body-weight increased 6.0 g for every 100 kJ/m^2 increase in food availability (r^2_{54} = 0.226, P < 0.0001; Fig. 5.3); male body-weight increased 2.1 g for every 100 kJ/m^2 increase in food availability (r^2_{58} = 0.288, P = 0.008).

Over the entire study period, however, food availability had only a slight and nonsignificant effect on body-weights. This lack of response later in the season was probably due to the energetic requirements of incubation and, especially, chick-rearing, when body-weights of both sexes were low (see Fig. 5.2 for females, and Chapter 1 for both sexes).

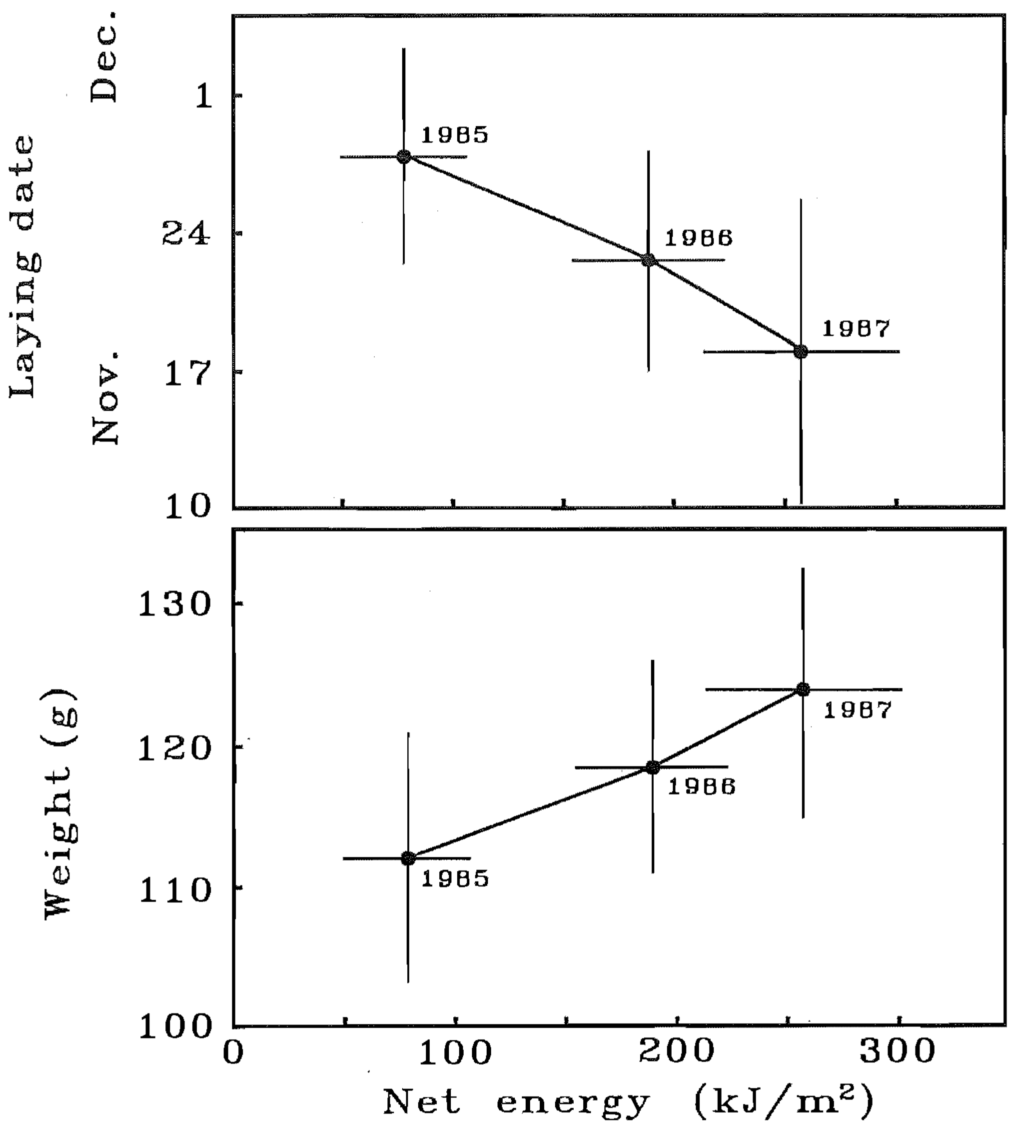

Figure 5.3. The effect of between-season differences in food availability in November on mean female snipe body-weight and the date when laying started. Food availability increased sequentially from November 1985 to November 1987 (Table 5.3). Body-weights based on samples of 16 females in November 1985, 17 in November 1986, and 23 in November 1987. Laying date is the mean date of first-egg laying for the first five females to breed in the study area each year (see Methods). Error bars represent one standard deviation of the mean.

Food availability and the timing of breeding

The date of initiation of laying by snipe over three breeding seasons was correlated with mean food availability in November (r^2_{13} = 0.356, P = 0.008; Fig. 5.3). When food was more abundant, females reached threshold laying weights earlier. Those females that laid early were able to complete incubation at about the time that food availability peaked in mid to late December (Figs 5.4 & 5.5). The remaining 50 - 60% of broods hatched in January and February, when food availability remained high. In both 1985-86 and 1986-87 food availability was higher during chick-rearing than during the preceeding six weeks (t_{34} = 2.76, P = 0.009).

Survival from hatching to age one-year did not differ between early-hatching (older than 30 days at my departure) and late-hatching chicks (X^2 = 0.004, n.s.; Chapter 1), suggesting that there was little advantage to breeding early. However, those snipe that laid early had more time for a second breeding attempt if the first failed. Clutches that failed after 8 January were not replaced (Chapter 1).

Factors controlling the end of laying were not determined. By mid-February, all failed female breeders had started to moult, and had refeathered brood patches and low body-weights (< 123 g). I assumed that laying did not occur after mid-February, but I left the island on 10 March 1986 and 20 February 1987. Three of the nine nests containing eggs in the middle two weeks of February 1987 were deserted, suggesting that the adults were in poor physical condition and unable to complete incubation. No other desertions were recorded during this study. While there was a decline in food availability in mid-February 1987 (Fig. 5.5) there was no way of knowing whether this represented the end of the summer plateau in food abundance. Food availability remained high in late February 1986 (Fig. 5.4).

Food availability, weather conditions and chick mortality

Deaths of chicks were not correlated with rainfall, temperature, food availability in the week of death, or food availability in the preceeding two or three weeks (Table 5.4). Multiple regression analysis did not reveal any relationship between combinations of these variables and chick mortality (Table 5.4). This was partly explained by the stability of environmental conditions in 1985-86 and 1986-87; rainfall, temperature and food availability did not show any marked fluctuations during the chick-rearing period. As hatchings were not synchronous (Figs 5.4 & 5.5)

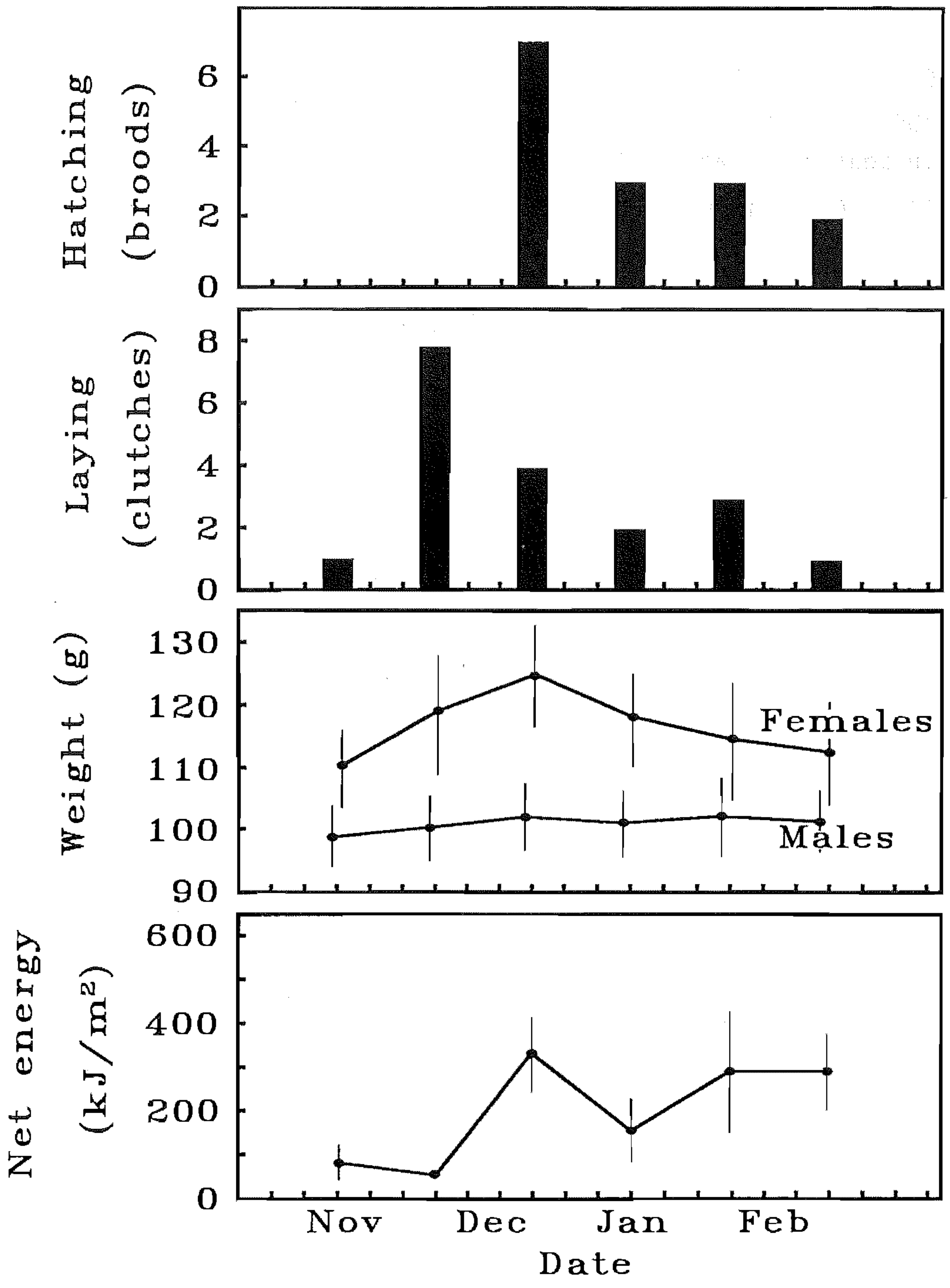

Figure 5.4. Food availability, adult snipe body-weights, laying and hatching per three-week interval in the study area, 1985-86. Error bars represent one standard deviation of the mean. The first clutches hatched when food availability peaked in late December. The remaining clutches hatched while food availability remained high in January and February.

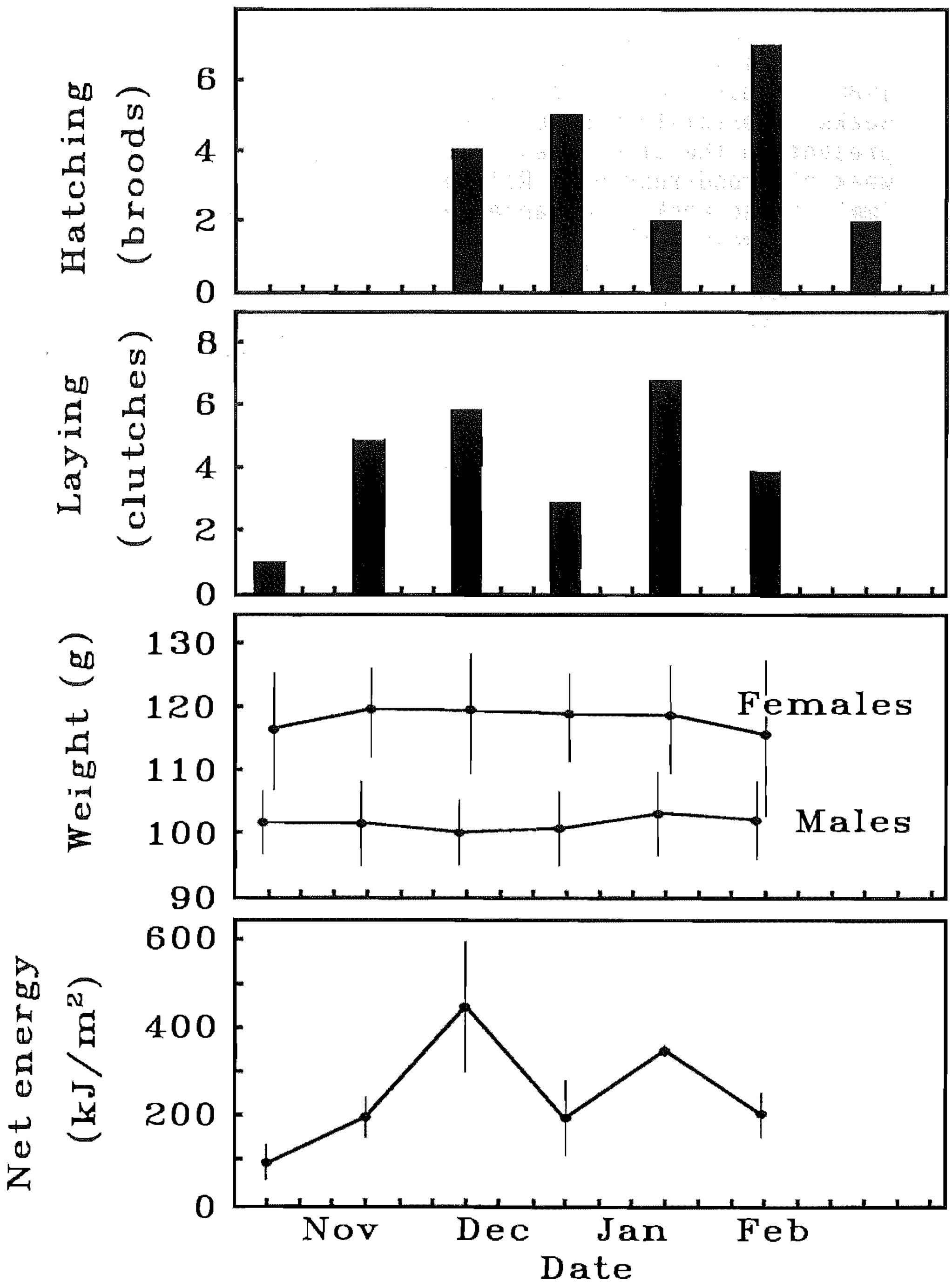

Figure 5.5. Food availability, adult snipe body-weights, laying and hatching per three-week interval in the study area, 1986-87. Error bars represent one standard deviation of the mean. The first clutches hatched when food availability peaked in mid-December; hatching continued through January and February.

Table 5.4. The effect of rainfall, air temperature and food availability on snipe chick mortality, 1985-86 and 1986-87, based on the disappearances of 21 chicks over 23 weeks. Mortality was measured as the percentage of chicks present in the study area that disappeared during each week of brood-rearing. Rainfall (Rain) = total rainfall (mm) in the week of disappearance (death), Temperature (Temp) = mean daily air temperature (°C) in the week of death, Net energy 1 (E1) = mean food availability (kJ/m^2) in the week of death, Net energy 2 (E2) = mean food availability (kJ/m^2) in the two weeks preceeding and including the week of death, Net energy 3 (E3) = mean food availability (kJ/m^2) in the three weeks preceeding and including the week of death. Chick mortality rates were not explained by any combination of these environmental variables.

	Residual mean square	df	*r*	F	Significance
Rainfall	549.5	21	-0.101	0.219	0.805
Temperature	552.4	21	-0.072	0.110	0.896
Rain + Temp	573.3	20	-0.017	0.170	0.916
Net energy 1	551.2	21	-0.086	0.156	0.857
Net energy 2	515.1	21	0.269	1.638	0.218
Net energy 3	540.9	21	0.161	0.557	0.581
E1 + Rain	574.9	20	-0.118	0.142	0.934
E1 + Temp	575.4	20	-0.114	0.113	0.940
E1 + Rain + Temp	601.1	19	-0.143	0.133	0.968
E2 + Rain	529.0	20	0.304	1.002	0.404
E2 + Temp	539.8	20	0.272	0.801	0.508
E2 + Rain + Temp	555.8	19	0.307	0.660	0.627
E3 + Rain	560.3	20	0.197	0.405	0.751
E3 + Temp	567.9	20	0.161	0.267	0.848
E3 + Rain + Temp	589.6	19	0.198	0.259	0.900

and most chick deaths occurred on the day of hatching (Chapters 1 & 3), dates of chick mortality were spread throughout the summer. Peaks in chick mortality reflected peaks in hatching rather than environmental factors. Adult snipe were seen to brood chicks in the nest for longer than normal during rainstorms (Appendix 2) indicating that behavioural responses of adults may counteract minor environmental perturbations.

The high mortality of newly-hatched chicks (n = 17, 35% of chicks), plus two chicks that died while hatching (Chapter 1), suggests that snipe chicks had low energy reserves at hatching. Causes of chick mortality were not determined, as no dead chicks were found. Predation can be discounted, as potential predators are absent from the Snares Islands (Chapter 1). Guthrie-Smith (1936) reported moribund chicks from nests of Stewart Island Snipe *C.a. iredalei*, and considered it "to be the custom" for the parents to abandon one chick at hatching.

Discussion

Food availability and the timing of breeding

Historically, reproductive ecologists have argued that food supply constrains both mating opportunities (Emlen & Oring 1977, Oring 1982) and reproductive success (e.g. von Haartman 1971, Ankney & MacInnes 1978). The high level of parental investment by both sexes of New Zealand Snipe limited opportunities for access to additional mates. High parental investment and low potential reproductive success per pair were both features of a breeding system presumed to have evolved in response to low food availability in a stable environment (Chapter 1). Given that the breeding system of New Zealand Snipe appears to be food limited (see Introduction), how did variation in food availability affect their breeding?

The timing of laying by snipe was determined by the proximate stimulus of food availability; female body-weight was positively correlated with food supply at the start of the breeding season, and females reached a body-weight in excess of 140 g before they laid. Consequently, snipe bred earlier in years when November food availability was higher. Those females that did not lay were never recorded to exceed 122 g, suggesting that the decision to breed or not to breed was determined by the body condition of the female (see also Drent & Daan 1980). Food availability may also have determined the cessation of laying, as no female heavier than 122 g was captured after the last clutch was laid each year.

Högstedt (1974) similarly reported that the length of the pre-laying period in Lapwings *Vanellus vanellus* was highly and negatively correlated with earthworm abundance. Earlier laying was associated with increased food in 23 of 39 studies reviewed by Martin (1987) and Arcese & Smith (1988). These findings in themselves do not refute Lack's (1968) hypothesis that birds should rear young when food is most abundant; if the annual peak in food abundance followed the initial increase in food abundance by a time equal to the time required for oogenesis and incubation, then food supply could provide both proximate and ultimate control over the timing of birds' breeding seasons (Perrins 1970).

The start of hatching for snipe coincided each year with the most pronounced peak in food availability (Figs 5.4 & 5.5) and hatching continued while food availability remained high. Chicks were reared when food was most abundant, as predicted by Lack (1968). Maxson & Oring (1980) and Lank *et al.* (1985) reported similar findings for Spotted Sandpipers *Actitis macularia*. They recorded a bimodal pattern of food abundance; the first females to lay did so during the first food peak, and their eggs hatched during the second food peak three weeks later. The onset of egg-laying varied from year to year in association with food abundance (Lank *et al.* 1985), but after laying began there was no relationship between food abundance and the number of eggs laid (cf. my Figs 5.4 & 5.5). Maxson & Oring (1980) reported food abundance (dry weight) in their study area to vary up to 71 fold within each breeding season, compared with a six fold variation in this study (Fig. 5.1). These two scolopacid species breed in very different environments (Spotted Sandpiper with superabundant food, New Zealand Snipe with low food) and have totally different breeding systems (polyandrous Spotted Sandpipers can lay up to 20 eggs in a season, Lank *et al.* 1985, cf. a maximum of four eggs for New Zealand Snipe, Chapter 1) and yet both species provide evidence that food abundance during egg formation acts as a predictor for high food abundance during chick-rearing three weeks later.

Food availability versus food abundance

This study is unique among studies of food supply and breeding by birds in that it includes an estimate of the cost of obtaining food. The composite variable 'Food availability' (kJ/m^2) was determined by both 'Food abundance' (kJ/m^2) and 'Cost of extraction' (kJ/m^2). I was able to estimate the 'cost' of prey capture by snipe because of the stereotyped feeding method of snipe - all food was captured by probing. Other species that could be studied using this technique include other snipe and woodcock species (all year round), plus godwit, curlew and sandpiper species on their nonbreeding grounds. Green (1988) considered both prey abundance and soil penetrability when investigating environmental factors affecting the timing of breeding by Common Snipe *Gallinago gallinago*, but he considered them as separate variables (measured in g wet weight and kg respectively) rather than merging them into a single measure of food availability.

Soil penetrability had very little effect on food availability for snipe on the Snares Islands; penetrometer readings were consistently low in all habitats and in all sampling periods. Even in habitats with low food abundance, the mean cost of extraction never exceeded 1% of the mean food abundance (Table 5.2). Soil penetrability may have more influence on food availability in winter, depending on how low food abundance becomes.

Weather conditions and food availability

The relationships between rainfall, temperature and food availability shed some light on how the severe weather conditions in 1982-83 may have influenced food availability (Chapter 4). While small variations in rainfall and temperature within breeding seasons had little effect on food availability (Table 5.2), between year variation in weather conditions at the start of the breeding season appeared to affect the timing of peaks in food availability; in years with high temperatures and low rainfall, food availability in November was higher (Table 5.3). Perhaps the low temperatures and high rainfall (3.6 times the mean for the succeeding four summers) in 1982-83 dampened the magnitude of the summer peak in food abundance. Food abundance in Mud declined with increasing rainfall (Table 5.2). In 1982-83 the entire study area was continuously muddy (Johns *et al.* 1983, pers. obs.); high soil water content may have reduced food abundance for snipe in all foraging substrates.

Environmental stability and the breeding system of snipe

The Snares Islands are a very stable ecosystem; there was little fluctuation in weather conditions and food availability both within and between seasons. During six years of fieldwork, the only major environmental flux coincided with the 1982-83 El Niño event - the strongest oceanographic disturbance in the eastern Pacific this century (Chapter 4, Cane 1983). Environmental stability is likely to have been one of the factors that has led to the highly *K*-selected breeding system of New Zealand Snipe (Chapter 1).

Within each breeding season, food availability fluctuated less than 56% once the initial peak in food availability was reached (Figs 5.4 & 5.5). The long plateau in food availability each summer may have led to the rather asynchronous breeding season of New Zealand Snipe: laying in three seasons extended over 71 - 89 days (Appendix 2). Chicks raised early or late in the season had equal chances of surviving to one-year, indicating little advantage to breeding early, especially given the high rate of nest success (Chapter 1). Environmental stability, acting through asynchronous hatching as well as the relatively constant weather conditions and food availability, was also considered the most likely explanation for the absence of association between dates of chick death and minor fluctuations in rainfall, air temperature and food availability.

General discussion and conclusions

Food availability, intraspecific competition and breeding

On the Snares Islands, New Zealand Snipe *Coenocorypha aucklandica* have few biotic constraints on population size. The terrestrial ecosystem has a simple structure, with low species diversity of vascular plants (Fineran 1964, 1969) and of breeding landbirds (Warham 1967, Williams 1981). Terrestrial mammals are absent, and no resident predatory birds specialise on landbirds or their nests (McLean & Miskelly 1988). The snipe is the only resident landbird on the Snares Islands that feeds exclusively on soil-dwelling invertebrates, and it is also the only species that forages at night as well as by day. Snipe on the Snares Islands are not preyed upon at any stage of their life history, and they have no foraging competitors other than conspecifics. In addition, I never saw a diseased bird in six years of field work. In the absence of predation, interspecific competition and disease, the only biotic factor likely to limit the snipe population on the Snares Islands is intraspecific competition for food, mates and territories (see Lack 1954, Krebs 1978, Stamps & Buechner 1985). The high population densities, high hatching success, and high survival rates of adult and juvenile New Zealand Snipe are attributed to the absence of predators (Chapters 1 & 3).

Theoretical ecologists have argued that species which live in stable environments will be at saturation densities, near the carrying capacity *K*, and will be subject to density-dependent controls (e.g. predation, food shortage and disease) rather than density-independent controls (mainly climate)(see MacArthur 1962, Cody 1966, Krebs 1978, Ricklefs 1980). The environment that snipe inhabit on the Snares Islands is very stable, with little within-year variation in rainfall and temperature (New Zealand Meteorological Service 1972), and little within- and between-breeding season variation in rainfall, temperature and food availability (Chapters 4 & 5). Density-dependent mortality during the nonbreeding season (see Chapter 3) and an extremely *K*-selected breeding system (see Chapter 1) are prima-facie evidence that New Zealand Snipe are limited by food availability through intraspecific competition.

Reduced clutch size and high parental investment per offspring are characteristic of almost all insular bird species (reviews in Cody 1966, 1971, Stamps & Buechner 1985). As most insular landbirds also occur at high densities (see Stamps & Buechner 1985), a small clutch may be a consequence of high population density, rather than an insular effect *per se*. Species that are limited by density-dependent processes should reallocate reproductive energy into producing fewer, more competitive young; i.e. food limitation at high population densities is the ultimate cause of small clutch sizes (Cody 1966). That food limitation reduces clutch size at high population densities was demonstrated experimentally by Arcese & Smith (1988). They supplied supplementary food to selected pairs in a dense insular population of Song Sparrows *Melospiza melodia*, and found that experimental birds laid earlier, laid larger clutches and produced more independent young than controls. Arcese & Smith concluded that clutch size was controlled by the amount of food available for each pair, therefore low reproductive output when at high densities was due to intraspecific competition for a limited food supply.

New Zealand Snipe had lower potential reproductive output, and higher parental investment than any other scolopacid for which information is available. Compared with Common Snipe *Gallinago gallinago*, New Zealand Snipe had courtship-feeding, large eggs, a long egg interval, a small clutch, shared incubation, a long incubation period, slow chick growth rates, a long period of chick dependence, and a long relaying interval following breeding failure (Chapter 1).

A major problem with any comparative study of reproductive ecology is choosing a suitable species or population for comparison (Lack 1968, Woinarski 1985). All extant populations of *Coenocorypha* snipes are confined to small oceanic islands that resemble the Snares Islands in lacking potential predators and competitors, hence intraspecific or intrageneric comparisons are of limited value when investigating ecological correlates of breeding systems. Of the 19 remaining species (3 genera) in the subfamily Gallinagininae, the Common Snipe is the only species for which the breeding system is well known (Chapter 1). However, there are two possible reasons why Common Snipe may not be an appropriate species for comparison of breeding ecology with New Zealand Snipe:

(1) *Environmental differences*. Common Snipe inhabit very different ecosystems to New Zealand Snipe. Most detailed studies of Common Snipe breeding ecology have been carried out in Britain (e.g. Green 1985a, 1988, Green *et al.* submitted MS) and in North America (e.g. Tuck 1972), where snipe must contend with high seasonality, a variety of indigenous mammalian and avian predators, hunting, migration, and potential competition from sympatric scolopacids. Differences in the breeding systems of New Zealand and Common Snipes may reflect a suite of environmental differences, both biotic and abiotic, rather than being due

to a single factor.

(2) *Phylogenetic differences*. Although no-one has estimated how long the genera *Coenocorypha* and *Gallinago* have been separated, *Coenocorypha* is often considered an ancient, generalised form, with *Gallinago* a derived, specialised form (Lowe 1915, Tuck 1972, Strauch 1978). Lowe even referred to the Chatham Island Snipe *C. pusilla* as a "living fossil". Differences in the breeding systems of *Coenocorypha* and *Gallinago* could be due to *Coenocorypha* retaining plesiomorphic characters that have been lost by *Gallinago*, or *Gallinago* may have autapomorphic characters evolved since the split with *Coenocorypha*. This interpretation is untenable on two counts. Firstly, all members of the four scolopacid genera that breed south of the equator lay clutches of only 2-3 eggs (Table 1); a small clutch must have evolved at least four times independently, as the nearest relatives of each group contain species with the 'ancestral' (sensu Maclean 1972) 4-egg clutch. Secondly, some features of the breeding systems of *Coenocorypha* snipes have not been reported for any other scolopacid (e.g. courtship feeding, 3-day egg interval, prolonged feeding of chicks by adults; Chapter 1). Gallinagininae are a specialised branch of the Scolopacidae (Strauch 1978), therefore snipe species are unlikely to have plesiomorphic characters that are not found in any other member of the family.

The unusual features of the breeding systems of *Coenocorypha* snipes are best interpreted as adaptations that have arisen as evolutionary responses to intraspecific competition for food in a stable environment. Food availability also limited breeding proximately; female body-weights (and laying dates) were strongly correlated with November food availability, and hatching was coincident with peaks in food abundance (Chapter 5).

Competition for mating opportunities

Food was not the only resource that New Zealand Snipe competed for; territories and mates were also limiting (Chapter 3). A high proportion of resident males was unable to obtain territories, as the entire study area was divided into contiguous territories by alpha males. In Chapter 3, I argued that subordinate male snipe were tolerated within territories because they had nowhere else to live, and because it was not energetically feasible for alpha males to evict persistent, cryptic intruders. A topographically fixed territory was a prerequisite for obtaining a mate, but males that had territories and mates defended only the female, and not the food resource within the territory.

The high level of parental investment by both sexes of New Zealand Snipe (i.e. courtship feeding, shared incubation and prolonged chick-rearing by both sexes) placed severe constraints on additional mating opportunities (see Emlen & Oring 1977). Males were unable to assist with more than one nest (or brood) at a time (Chapter 2), and few unpaired females attempted to incubate alone. The time and energy constraints of chick-rearing prevented alpha males from maintaining their territories, and so subordinate (beta) males were able to gain territories (albeit temporarily) and court receptive females.

The one-chick-one-parent system for brood-rearing by New Zealand Snipe permitted some flexibility in reproductive output. Failed breeders (singly, or as a pair) always evicted any subordinate birds that had claimed their previous territory, and hence were able to renest (with either the same mate or a new mate). In theory, it would be possible for a sequentially polygynous or polyandrous bird to produce three fledglings (c.f. a maximum of two for a monogamous pair) if its first mate continued rearing a chick, and if the second breeding attempt produced two chicks. This was never observed, but one female that lost her first chick still produced two fledglings (one from each brood).

Common Snipe may have a territorial system similar to that for New Zealand Snipe, as Tuck (1972: 138) records: "Unless a snipe makes itself conspicuous by calling continuously or by some form of agonistic display, it is allowed to trespass in another's territory without being challenged. A trespassing male which calls insistently quickly elicits response...and the intruder is soon harassed and put to flight". Male Common Snipe also assist with brood-rearing, although they do not incubate. Tuck (1972: 137-138) further reports: "During the late stages of incubation, part of the territory occupied earlier may be usurped by another bird...the first male soon becomes involved with the hatching and care of the chicks and no longer actively defends his former territory. The activity at this time, by late-prospecting birds, may account to some extent for the supposed sexual resurgence in snipe reported by several authors...five marked individuals recaptured in pre-empted territories had all been banded as chicks the previous summer and were yearlings breeding for the first time". Tuck does not explicitly state that these males were associated with nests, but these anecdotal observations suggest that the mating systems of New Zealand and Common Snipes are similar.

Summary of factors constraining breeding by New Zealand Snipe

The size of the breeding population of New Zealand Snipe was determined by density-dependent mortality during the previous winter (Chapter 3). Many birds (predominantly one- and two-year-olds) were unable to obtain territories or mates due to exclusion by dominant males. A higher proportion of birds was excluded from breeding in years of high population density. Most matings were monogamous as high parental investment by both sexes precluded additional mating opportunities. The two polygynous males did not produce many more offspring than monogamous males, as breeding success of females that incubated unaided was very low (one successful nest from four known attempts; Chapter 2).

Increasing food availability at the start of the breeding season was a proximate stimulus for laying (Chapter 5). Female body-weights and laying dates were highly correlated with November food availability; females reached a threshold body-weight of c.142 g before laying. The 32% of paired females that did not lay were never recorded as weighing over 122 g.

Each pair of snipe had very low potential reproductive output, as the 2-egg clutch and the long period of chick dependence did not allow sufficient time for two broods to be reared in a season. Hatching success was 80%; most failures were due to desertions during periods of low food availability. Chick mortality on the day of hatching was 35%, but was not correlated with fluctuations in food availability or climatic conditions. Chick survival subsequent to hatching was high (Chapter 3), and 46% of fledglings (30+ days old) were recaptured in following years.

Breeding birds were highly faithful to their territory and mate between seasons, regardless of their breeding success the previous year (Chapter 3). Hence, young birds could only enter the breeding population if a paired bird died. Although males and females were physiologically capable of breeding in their first year, most did not get an opportunity to breed until two- or three-years-old. Nonterritorial males that maintained a home range including part of a territory always succeeded in gaining the territory if it became vacated, either temporarily (during chick-rearing of the original territorial pair) or permanently (following death of the previous owner).

Although the snipe population on the Snares Islands was predominantly controlled by intraspecific competition for food, mates and territories, the abnormal weather patterns associated with the 1982-83 El Niño event had a marked effect on natality and mortality (Chapter 4). The population reached its lowest recorded density (5.4 birds/ha) in the breeding season following the El Niño. These findings support the hypothesis that landbird populations on oceanic islands are limited by intraspecific regulatory processes, while recognising that occasional stochastic events (in this case climatic) can also limit populations.

Implications for management of New Zealand Snipe

The present distribution of New Zealand Snipe is only a fraction of their former range. Snipe became extinct on the New Zealand mainland during Polynesian colonisation, and have disappeared from at least 14 different islands since AD 1800. These extinctions have been attributed to the introductions of kiore *Rattus exulans*, ship rats *R. rattus*, cats *Felis catus*, pigs *Sus scrofa* and Weka *Gallirallus australis*, or a combination of these species (Appendices 1 & 3, Miskelly 1987, Galbreath & Miskelly 1988, Holdaway 1989). However, all surviving forms of New Zealand snipe have substantial populations on island Nature Reserves that are free of introduced predators.

While none of these snipe populations is , to our knowledge, declining, there is no room for complacency regarding their future survival. Bitter experience has taught us how rapidly ship rats can eliminate snipe on an island considerably larger than the Snares Islands (Appendix 1, Bell 1978). The first requirement of a management plan for snipe is to ensure that potential predators (particularly rats and cats) do not colonise snipe islands. Barring such ecological catastrophes, there should never be a need to actively manage snipe on the islands where they currently occur, as the snipe are already at carrying capacity, and the populations are self-regulatory.

However, there are at least five compelling reasons why snipe should be reintroduced to islands where they once occurred, or perhaps to islands where they may have occurred, if these are clear of predators. Potential benefits include: (1) reducing the chances of an ecological catastrophe eliminating one of the populations, (2) restoration of a pre-existing ecosystem, (3) genetic conservation, (4) educational assets - few people ever get to see a New Zealand Snipe, and (5) aesthetic benefits (see Atkinson 1988).

This study has established that snipe on the Snares Islands are limited by intraspecific competition, and that a large proportion of the population are excluded from breeding each year. These 'surplus' birds (mainly one- and two-year-olds) could be transferred to a new habitat without detriment to the breeding population on the Snares Islands. Indeed, reducing the population density on the Snares should enhance survival and reproductive success of the remaining birds (Chapters 1 & 3).

Recognition of subordinate birds would require intensive study of a marked population before a transfer was planned. However, removal of a 'random' sample of snipe from all social classes probably would not disrupt the social structure, as gaps in the breeding population were filled rapidly in this study.

Establishment of a snipe population on a new island would provide an ideal opportunity to test some of the conclusions of this study. Snipe at low density in an environment with a previously unexploited food resource would be expected to have higher survival rates, lay larger clutches, have a shorter egg interval, have higher hatching success, have faster growth rates, breed at a younger age, and perhaps be able to breed more than once in a season. Lower population density could also create a more labile social structure, with lower rates of territory and mate fidelity, and longer natal dispersal distances.

Acknowledgements

This study was funded primarily by a National Parks & Reserves Scholarship from the Department of Lands & Survey (now Department of Conservation) and was supervised by Dr Ian McLean. The Department of Lands & Survey and Department of Conservation issued permits to enter and carry out research on the Snares Islands Nature Reserve and Rangatira Island Nature Reserve, and also met most transport and living costs incurred during the expeditions. Additional financial assistance was received from the Royal Forest & Bird Protection Society of New Zealand, the Ornithological Society of New Zealand, the New Zealand Wildlife Service, and my parents.

A field-based study in areas as remote as the Snares and Rangatira Islands can only succeed with the help of many people. Academic and technical staff from Zoology Department, University of Canterbury, assisted with organising equipment, food, transport and people; thanks are due to Peter Johns, Jack Kay, Ian McLean and (especially) 'Saint' Bruce Lingard. The task of arranging transport to and from islands varied between easy and impossible, depending on the activities of fishing boats around the islands. Many different vessels were used: F.V. *Sea Emerald* (5x), F.V. *Savannah* (3x), F.V. *Sea Way*, F.V. *McLachlan*, M.V. *Acheron* (3x), M.S. *Lindblad Explorer* (2x) and M.S. *World Discoverer* for transport to and from the Snares, and F.V. *Lady Rhonda* (4x), F.V. *Miss Rachel* (2x) and F.V. *Taiko* (2x) for transport within the Chathams. Voyages varied in their degree of comfort in parallel with sea conditions, but were always memorable. Especial thanks to Kevin Schofield (*Sea Emerald*) and Ian Leask (*Savannah*) for their hospitality, generosity and interest over several years. The staff, crew and passengers on the *Lindblad Explorer* and *World Discoverer* willingly provided brief (and free) tastes of luxurious living far beyond the means of depauperate research students.

All 36 fellow expedition members shared the burden of daily duties, and (almost always!) provided an atmosphere of good will and comradery that enhanced my enjoyment of time spent on the Snares and Chathams. Most expeditioners regularly reported sightings of banded snipe; Gillian Eller received a gold star for her diligence in my absence during most of the 1983-84 season on the Snares. Richard de Hamel, Grant Harper, Evert Kampert, Ian McLean, Brian Rance, Paul Sagar, Garry Scrimgeour, Alan Tennyson and Joe Waas helped at various times with capturing snipe. Alan, Evert (2) and Grant picked up extra Brownie points for finding snipe nests. Evert also reduced the tedium of soil sampling during most of the 1986-87 season.

Invaluable assistance throughout my time at Canterbury has been provided by the technical staff in Zoology Department, most of whom have lent a willing hand or advice somewhere along the line: Franz Ditz and Tas Carryer designed and built the amazing incubation-constancy recorder at unreasonably short notice (and it worked perfectly); Gavin Robinson fixed the bomb calorimeter after a couple of less-than-controlled explosions; Dave Greenwood, Bruce Lingard and Sandy Gall found practical solutions to many problems beyond my ken; Joan Buckley cheerfully provided advice and equipment for illustrations, and Terry Williams printed all the black & white photographs in the thesis. Jan McKenzie always found time for help and encouragement, no matter how urgent her own work.

Unpublished data were generously provided by Mike Dennison, Cameron Hay, Bruce Keeley, Les McPherson, Don Merton, Rod Morris, Ron Ordish, Hugh Robertson, Paul Sagar, Gillian Thompson, John Warham and Peter Wright.

Many of the ideas presented here have been developed during informal discussions with colleagues within Zoology Department, and at Behaviour and Ecology Workshops. It is always hard, in retrospect, to recognise where and when the seed of an idea was sown, but I acknowledge the fertile environment (make of it what you will) provided by conversations with Ian McLean, Peter Carey, Richard Holdaway, Ian Jamieson, Henrik Moller, Simon Pollard, Roger Reeves, Richard Rowe and (particularly) Paul Sagar and Joe Waas. Ian McLean, Allen Rodrigo, Kelly Duncan, Richard Rowe, Richard Holdaway and Tom Matheson assisted with untying statistical and computational tangles.

Paul Sagar acted as unofficial supervisor during this project; on the Snares, in Christchurch, and on many field trips throughout New Zealand. With characteristic good humour, Paul provided insightful (and often witty) comments on all the papers presented here; I thank him for his enthusiasm and industry. Thanks also to Joy Sagar for her friendship and hospitality.

A debt of thanks goes to Lyn de Groot and (especially) Tracey Robinson for the many hours that they have spent helping me with typing and word-processing - this thesis would have been a lot shabbier without them. Various sections benefitted from comments by Joe Waas, Peter Bergstrom, Peter Carey, Kelly Duncan, Rhys Green, Barrie Heather, Curt Lively, John Warham and Kathy Winnett-Murray. Ian McLean and Paul were the only ones subjected to criticising the lot; I thank them for never admitting that they were sick of reading about snipe. Thanks also to Carolyn Fry for proof-reading all the final versions.

Peter Carey, Joe Waas and ANARE provided the perfect incentive for me to pull-finger and finish writing. Thanks to Pete for encouragement throughout the final weeks (and the occasional good set), but especially for doing the lion's share of organising our Antarctic sojourn while I concentrated on writing. My greatest debt is to Carolyn, who after years of putting up with my prolonged absences and unreasonable work hours had to face the injustice of my departure for five months, mere hours after submitting this.

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Appendix 1

The identity of the Hakawai.

Notornis 34 (1987): 95-116.

Reprinted from NOTORNIS Vol. 34, Part 2, June 1987: pp 95-116

THE IDENTITY OF THE HAKAWAI

By C. M. MISKELLY

Booklet to accompany thesis by Colin M. Miskelly "Social and Behavioural constraints on Breeding by New Zealand Snipe"

THE IDENTITY OF THE HAKAWAI

By C. M. MISKELLY

ABSTRACT

The hakawai was a 'mystery bird' formerly found on islands off Stewart Island; although never seen, its startling call was heard at night. The call of the hakawai, and its distribution and decline are described. The hakawai (under several spelling variations) is widely mentioned in myths and legends of the Maori throughout New Zealand; these records are summarised and the various theories for the hakawai's identity are discussed.

Evidence for non-vocal aerial displaying by New Zealand snipe *(Coenocorypha)* is presented. The hypothesis that the hakawai was an aerial display of Stewart Island Snipe *(C. aucklandica iredalei)* was investigated by comparing the distribution and decline of snipe with that of the hakawai, and by playing a tape recording of an aerial display of Chatham Island Snipe *(C. pusilla)* to people who had heard the hakawai. These data support the hakawai = snipe hypothesis. The historical distribution of Stewart Island Snipe included Big South Cape, Pukeweka, Solomon, Poutama, Jacky Lee, Herekopare, Ruapuke and Green Islands in the last 100 years. The extinction of snipe on these islands is attributed to introductions of ship rats (*Rattus rattus*, two islands), weka (*Gallirallus australis*, four islands) and a combination of weka and cats (*Felis catus*, two islands).

It is proposed that subfossil remains of *Coenocorypha* from the North Island and the South Island be referred to *C. a. barrierensis* Oliver 1955 and *C. a. iredalei* Rothschild 1921 respectively.

INTRODUCTION

The early ornithological and anthropological literature of New Zealand contains many tantalising references to the birds encountered by the Maori before the arrival of Europeans. Many of the traditional oral accounts given describe species that are familiar to 20th century observers, but others can only refer to some of the 35 or so bird species known to have become extinct during about 1000 years of Polynesian colonisation up to AD 1800. While legends or descriptions of huge moa and the giant eagle *Harpagornis* have long captured the public's imagination, the recent interest in subfossil deposits of our smaller prehistoric inhabitants invites re-examination of accounts of less spectacular animals. Was kopa the extinct owlet-nightjar *(Megaegotheles)*? What of the poua on the Chatham Islands, or the mysterious ruruwhenua? (See Beattie 1954: 40.)

Trying to match fragments of an oral tradition with bone fragments of extinct birds is an intriguing pastime, but it is difficult to progress beyond speculation. However, not all mythical birds belong to such distant times. The hakawai was last reported in 1961 (Bell, B. D. & Merton, D. V. A classified list, with notes on the species, of birds of Big South Cape Island, April 1961. Unpubl. report NZ Wildlife Service). It is still fresh in the memory of many people who hold muttonbirding rights to the islands off Stewart Island. The story of the hakawai has an added piquancy; although many people can recall the loud, startling cry of the hakawai, the animal responsible has not been seen.

Many early ornithologists in New Zealand speculated on the identity of the hakawai, and muttonbirders are still interested. My interest in the hakawai arose through my research on New Zealand snipe *(Coenocorypha)*; the Stewart Island Snipe *(C. aucklandica iredalei)* was one of the many birds that had been suggested as the hakawai (Anon. 1931; Bell & Merton, unpubl.). After hearing aerial displays by Chatham Island Snipe *(C. pusilla)* on South East Island in December 1983, I collected data to test the hypothesis that the hakawai was the Stewart Island Snipe giving its aerial display. Much of the information in this paper was gleaned from conversations with muttonbirders in Southland and on Stewart Island in 1985, and from replies to questionnaires sent to muttonbirders from Kundy and Big Moggy Islands.

THE CALL OF THE HAKAWAI

Even on the few islands where it was known, the hakawai was rarely heard. The call was heard on calm moonlit nights and came from a great height. A human-like rendition of its name, *hakwai*, *hakwai*, *hakwai*, was followed by a considerable roar, as of a bird travelling at great speed "and this increases in volume as the descent is made until the air vibrates with it" (Anon. 1931).

My informants all agreed on the qualities of the first part of the call, but I received differing descriptions of the second (non-vocal) component. The most popular description of the call of the hakawai was that it resembled "a sound as if a cable chain was lowered into a boat" (Native 1931). Indeed, many people still refer to the hakawai as the chainbird. Some people familiar with the hakawai did not like this description and likened the sound to a "jet-stream" or "a blind rolling itself up" (Billy McQuarrie, pers. comm.) or "a shell passing overhead" (Rongo Spencer, pers. comm.).

Not all these differences are just personal differences in the interpretation of the same noise. Alan Skerrett (pers. comm.) thought that the hakawai call resembled a jet-stream sound but heard the 'rattling chain' occasionally as well: "Sometimes its rapid descent is accompanied by a rustling noise and sometimes by a chain sound" (Beattie 1954: 37). Bell & Merton (unpubl. report) ". . . never heard the so-called 'chain rattle' but once heard something approaching this".

However the hakawai's call was described, its effect on observers was fairly consistent. Many written accounts refer to physical reactions to the sound: "The next thing he knew he and his load of birds were mixed up together on the ground. He had fallen over in his fright". "I realized that I had heard the mystery bird and was off down the hill as fast as my legs could carry me, forgetting all about my stay at Te Maru" (Wilson 1979: 92). Several of the people that I spoke to remarked that they were very frightened of the "whizzing" noise.

Memories of the hakawai are kept alive not only by the mystery of its identity but also by the eerie quality of its sound and the web of myth and legend that has been spun around it.

MYTHS AND LEGENDS OF THE HAKAWAI

Although I have chosen to use the name hakawai, used by the southern muttonbirders, many variations in spelling and pronunciation are in the literature (Table 1). The usual variant is the northern Maori *hokioi*; the equivalence of the different names has been pointed out by Tregear (1897: 79), Best (1942: 152), Beattie (1954: 37), Reed (1963: 387) and Williams (1971: 33, 57 & 239). I will use hokioi or hakawai while discussing myths and legends to match the sources quoted; other variants will be given only in direct quotations.

TABLE 1 — Alternative spellings of 'hakawai'

hākuwai	White 1887; Best 1942 & 1982; Jenkin 1970; Williams 1971
hakuai	Tregear 1897; Pio 1901; Beattie 1954; Williams 1971
hakowai	Beattie 1954
hark-oh-why	Henderson 1981
hokiwai	Urumotu & Kerehoma 1872; Williams 1971
hokioi	Haast 1873; Tregear 1897; Best 1924 a & b, 1942; Reed 1961 & 1963
hokio	White 1885; Tregear 1897; Williams 1971
ōkio	Ngata 1970
okioi	Tregear 1897; Williams 1971

The hakawai was one of the 11 tapu (sacred) birds of Rakamaomao (the wind) and was said to have been a descendant of Tangaroa (god of the ocean) and Rehua (the star Antares, guardian of the uppermost heaven) (Best 1982: 265 & 563). In Maori legends and proverbs, the hakawai was a mythical bird dwelling afar in celestial space and only descending to earth at night. It was "the bird elusive and never seen, By the multitude in their thousands" (Ngata 1961: 261).

Several proverbs refer to the nocturnal habits of the hakawai, or its ability to conceal itself: "*Pekapeka rere ahiahi, hokioi rere po* (The bat flies at twilight, the hokioi at night)" (Reed 1963: 387); ". . . *ko taua manu he pena hoki me te Hokiwai, he manu whakangaro i tona tinana*" (that bird is like the Hakawai, it makes itself invisible) (Urumotu & Kerehoma 1872).

The hakawai lived in the heavens (White 1887: 130) and was considered the ancestor of ceremonial kites built by the Maori. A charm-song for an *aute* bird (kite built of paper mulberry) given by Pio (1901) finishes:

> *Pikitia e koe ki to matua, ki a Hakuai*
> *Ki to tupuna, kia Rehua i te rangi-e.*
> "Climb thou to thy ancestor, the Hakawai,
> To thy ancestor, Rehua in the heavens."

The most widely quoted legend about hokioi refers to a competition between hokioi and kahu (the hawk) to see who could fly the highest. This story explains why hokioi descends only at night and why he calls out his name. Different versions are given by Grey (1872), Best (1924a: 215-216, 1942b: 57 & 1982: 563-564) and Reed (1961: 193-194 & 1963: 387), but the legend is as follows:

> An argument arose between Kahu and Hokioi as to who could fly the highest. Kahu taunted Hokioi, saying that he could fly no better than Matata (the fernbird). This so angered Hokioi that he challenged Kahu to a trial, as to which could ascend the highest. Then both left the ground and flew to a great height. As he flew upward, Kahu kept continuous watch on the earth, as is his habit. Soon he saw some fern on fire and, forgetting the challenge, descended to prey on the creatures fleeing from the flames. Hokioi cried out to Kahu *He pakiwaha koe* ["You are a boaster"] then continued his flight until he lost sight of the earth. Hokioi never returned to earth again, but sometimes at night he is heard calling out his own name in derision of Kahu: *Hokioi! Hokioi! Hu!*

The last word *hu* represents the rushing sound of his flight, as heard by the Maori folk of this world.

> There is nothing to be seen, but you hear a cry, a dreadful laughter floating down from the heights. "Hokioi-Hokioi" is the cry, and as it ceases you hear that eerie whistle as a bird swoops down and up again into the blackness and silence of the night sky (Reed 1961: 193).

The legend gave rise to a proverb which is applied to boasters: *E hoa! He hakuwai te manu e karanga tonu ana i tona ingoa*. (Oh friend! The hakawai is the bird that is ever calling out its own name.)

To hear the cry of the hakawai was a bad omen. White (1885: 166) stated that the hakawai was heard on the eve of war, and that the cry was "caused by the choking of the bird with the hair of the heads of those warriors who are doomed to fall in the battle". In more recent times, the call of the hakawai was thought to forecast a southerly gale (Native 1931, Beattie 1954: 37, Jenkin 1970: 157); although it could be argued that bad weather will always follow a clear moonlit night in the stormy latitudes of the muttonbird islands.

Many muttonbirders believed that the hakawai could be heard only towards the end of the muttonbird season (May). From this arose the idea that the hakawai was the father of the muttonbirds *(Puffinus griseus)*, calling them away on their northern migration (Edwards 1954, Blackburn 1965). Some say that when the hakawai called all the muttonbirds came to the mouth of their burrows and listened (Beattie 1954: 38). The idea that the hakawai called only at the end of the muttonbird season is probably a result of observers being out at night mostly at the end of the season, when young muttonbirds come out of their burrows and can readily be caught. Earlier in the season, young muttonbirds are taken by day, from their burrows ('nanaoing'). Also, towards the end of the season most of the adult muttonbirds have departed on their northern migration, and so the nights are quieter and other sounds may be heard more easily. The muttonbirders are not on the islands from the end of May to mid-March.

Bell & Merton (unpubl.) heard hakawai in April, and Billy McQuarrie (pers. comm.) heard it in June. Several people that I spoke to thought the hakawai could be heard at any time of the year.

Kaiporohu told James Drummond that the hakawai lived in the clouds over Foveaux Strait, hovering invisibly (Beattie 1954: 36). Its call was first heard in the north, then in the south, east and west. The hakawai was thought always to fly in the same direction when giving its call, given as east to west for Herekopare Island by Dempsey (1967:96).

THE DISTRIBUTION OF THE HAKAWAI

The range of the hakawai had decreased steadily up to its disappearance in the early 1960s. Often information on the past distribution of the hakawai is vague, and it is difficult to assign dates to many records. The following summary starts with the most recent records and works back to pre-European days; this sequence roughly follows a south to north geographical sequence. Where possible, the decline of the hakawai on each island has been compared with the date of introduction of one or more of the following terrestrial predators: ship rat *(Rattus rattus)*, cat *(Felis catus)* and weka *(Gallirallus australis)*.

A. The islands off the south-west coast of Stewart Island

BIG SOUTH CAPE ISLAND

Big South Cape Island (Fig. 1D), the largest muttonbird island (930 ha), was long considered the stronghold of the hakawai. This was the only island where hakawai survived alongside the weka, which the muttonbirders introduced to many of the muttonbird islands for food and, on some, to control rodents.

Hakawai were usually heard over the low pakihi vegetation in the centre of the island, particularly between the two high points Mt Onion and Paopoko. I have one record of a hakawai being heard over the forested coastal slopes (Rongo Spencer, pers. comm.). On Big South Cape I. weka were mainly found under the forest (Guthrie-Smith 1936: 183, Richdale [no date a], Bell & Merton unpubl.) but have occupied the pakihi since the rat invasion (Bell, B. D. & O'Brien, J. F. O., 1964. Big South Cape Island, 16-28 April. Unpubl. report NZ Wildlife Service).

Hakawai were heard regularly on Big South Cape I. until the plague of ship rats which followed the 1963 muttonbird season. The last written report is that of Bell & Merton. No one has heard the hakawai since the rat invasion, although Noki Barrett (pers. comm.) claimed to have heard the first part of the call near the south end of the island in 1983.

POUTAMA ISLAND

Poutama Island, which lies 300 m south of Big South Cape I., held a hakawai population until at least 1931 (Anon. 1931). Native (1931) heard hakawai on Poutama on 10 May 1913, and Peter Beaton heard them during the 1920s (Jack McKay, pers. comm.). Jack McKay first went to Poutama in 1932 but did not hear hakawai there (although he heard them on Big South Cape I. in 1933). Weka had been introduced earlier to Poutama and were common in 1932. Ship rats reached Poutama in 1985.

SOLOMON ISLAND

Solomon Island (26 ha) lies about 200 m north of Big South Cape I. Hakawai were heard on Solomon I. in 1931 (Anon. 1931) and earlier (Eileen Willa, pers. comm.). I do not know whether hakawai were heard on Solomon I. after 1931. Weka have been there since at least 1913, when Guthrie-Smith

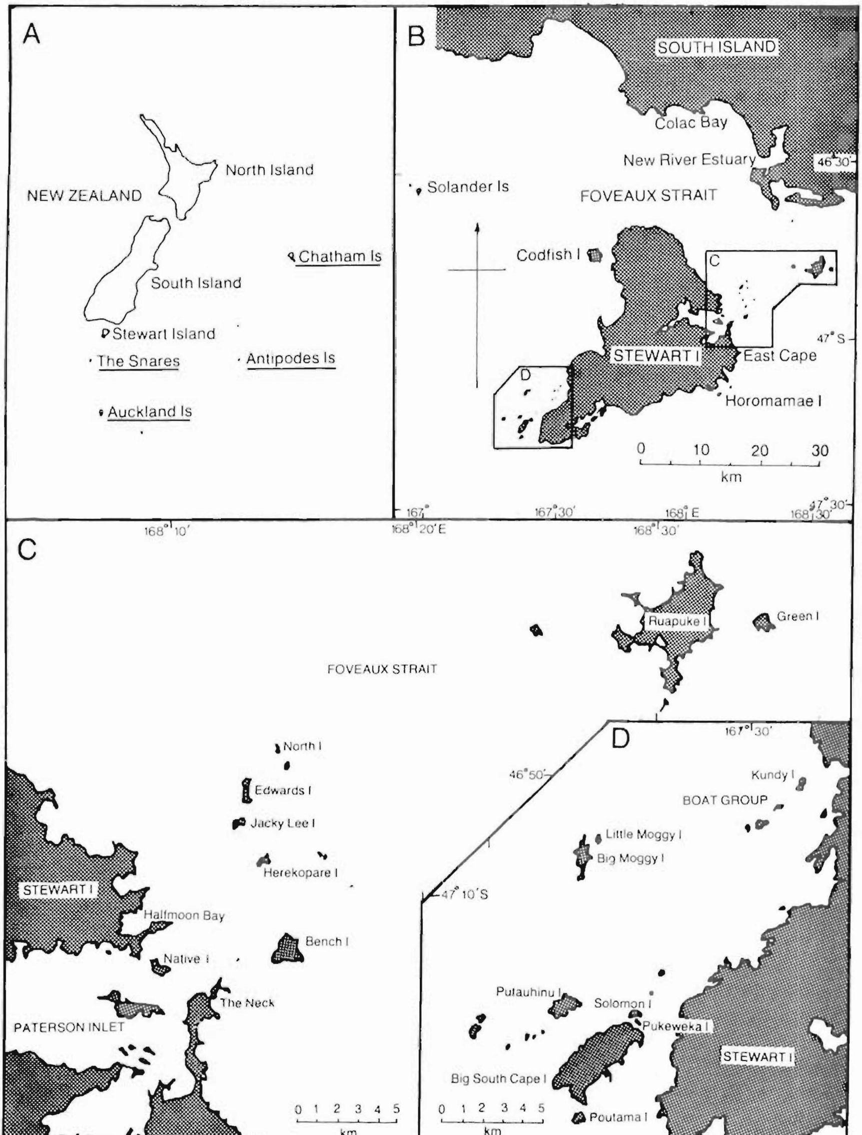

FIGURE 1 — Localities mentioned in the text. Those island groups underlined in 'A' still have snipe. There are reliable reports of hakawai from Ruapuke, Green, Jacky Lee, Herekopare, Solomon, Big South Cape and Poutama Islands in the last 100 years

(1925: 118) saw one or two pairs, but they are kept at a low density by the muttonbirders. Solomon I. was one of the three islands affected by the plague of rats in 1964.

BIG MOGGY ISLAND (MOKINUI)

Big Moggy Island is about 8 km north of Big South Cape I. Edwards (1954) stated that the hakawai "has not put in an appearance at Mokinui Island for some years". O. B. Nilsen (pers. comm.) informed me that his mother had heard a hakawai on Big Moggy Island "one very bright moonlight night, 40 odd years ago". Neither J. A. Hart (pers. comm.), who first visited the island in 1918, nor Patu King (pers. comm.), whose family started birding on Big Moggy I. in about 1890, had heard of hakawai being there.

Kiore *(Rattus exulans)* were already on Big Moggy I. in 1890, cats have been there since about 1915 and weka since before 1918 (J. A. Hart & Patu King, pers. comm.).

KUNDY ISLAND

Kundy Island (22 ha), one of four islands comprising the Boat Group, is about 15 km north-east of Big South Cape I. Russell Smith (pers. comm.) told me that hakawai had been heard there very occasionally in the past. Russel Trow (pers. comm.), who has been birding on Kundy I. since 1949 and whose grandparents birded there from 1905, was unaware of hakawai having been there.

Weka were introduced to Kundy I. in about 1947 (R. Trow, pers. comm.) and were removed by the NZ Wildlife Service in 1984. The island has no rodents.

B. Solander Islands

The Solander Islands lie about 60 km west-northwest of Stewart Island (Fig. 1B). Blackburn (1965) quoted a muttonbirder as saying that he had heard the hakawai on Big South Cape and Little Solander Islands in "recent years". None of the muttonbirders that I spoke to had heard of hakawai on the Solander Is, or of anyone staying overnight on Little Solander I.

I spent two nights on Little Solander I. (8 ha) in July 1985, but heard no hakawai. Solander I. (100 ha) has had weka on it for over 150 years (Cooper *et al.* 1986) but neither island has rodents.

C. The islands off the north-east coast of Stewart Island and in Foveaux Strait

HEREKOPARE ISLAND

Herekopare Island (28 ha) lies 8 km north-east of Halfmoon Bay (Fig. 1C). It is the only island away from the Big South Cape group that is generally recognised as a 'hakawai' island.

Three of the people that I spoke to had heard hakawai on Herekopare: Russell Smith and P. R. & E. Willa. Russell Smith, who first went to Herekopare as a young boy in the early 1920s, heard hakawai there only during the 1920s. The late P. R. (Buddy) Willa had heard the hakawai on Herekopare in the first decade of this century; Mrs Eileen Willa heard it during her only stay on the island, in 1924. Dempsey (1967: 95-97) also mentioned hakawai on Herekopare.

Guthrie-Smith is said to have heard the hakawai on Herekopare (R. Smith, pers. comm.; Dempsey 1967: 97). Although he stayed overnight on Herekopare in October and November 1911, he did not mention hakawai in his 1914 book.

Guthrie-Smith (1914: 15) heard one weka on Herekopare in January 1911, but the weka died out or were removed during the next muttonbird season (P. R. Willa, pers. comm.). Weka were reintroduced in the early 1920s (R. Smith & P. R. Willa, pers. comm.) but were not reported by Wilson (1959) when he and Edgar Stead visited Herekopare in 1932. Weka were apparently present in 1944 (see Fitzgerald & Veitch 1985) and were common in 1952 (Dempsey 1967: 87), but they were removed by muttonbirders before 1968 (Fitzgerald & Veitch 1985).

Cats were introduced to Herekopare in 1924 (P. R. & E. Willa, pers. comm.) and were exterminated by the NZ Wildlife Service in 1970 (Fitzgerald & Veitch 1985).

JACKY LEE ISLAND

Hakawai were 'formerly' heard on Jacky Lee Island (Bell & Merton unpubl.), which is 1.5 km north-west of Herekopare I. Weka, introduced to Jacky Lee I. some time after 1901, were common in 1932 (Wilson 1959: 60).

RUAPUKE ISLAND

Ruapuke is a large island in the eastern approaches to Foveaux Strait, 30 km north-east of Stewart Island. Hakawai were reported from Ruapuke last century (Billy McQuarrie, pers. comm.). The island, being farmed, presumably has cats. Weka are on Ruapuke (Watters 1963), and house mice *(Mus musculus)* colonised when the *Elizabeth Henrietta* ran aground on 25 February 1824 (McNab 1907: 236). Kiore have been reported (Atkinson 1978) but whether other rat species are present is not known. The presence of a colony of White-faced Storm Petrels *(Pelagodroma marina)* in 1941 (Wilson 1959: 105) argues against *Rattus* being there then, if current theories on petrels being vulnerable to rodent predation (Imber 1975, Atkinson 1985) are correct.

GREEN ISLAND

Green Island lies about 2 km east of Ruapuke I. Alfie Ryan told me that his grandfather had heard hakawai on Green I., probably late last century. It is one of the locations given by Beattie (1954: 37). Weka were present, but scarce, in 1941 (Wilson 1959: 110) and are still there (Thomas 1982).

D. The main islands of New Zealand

STEWART ISLAND

Native (1931) mentioned hakawai being heard at South and East Capes, and Dempsey (1967: 96) mentioned the East Cape of Stewart I.; they gave no dates. Weka are indigenous on Stewart I.; there are feral cats and all three species of rat (*R. exulans*, *R. rattus*& *R. norvegicus* – Taylor 1978).

SOUTH ISLAND

Billy McQuarrie and Mrs Eileen Willa both told me of very old reports of hakawai being heard at New River Estuary (Fig. 1B). Old Timer (1931) recalled hearing a hakawai at Colac Bay, Southland, in 1895; the local Maori at the time agreed that "one had never been seen on the mainland".

Henderson (1981: 221) gave an undated reference to a hakawai being heard (and seen) at Tasman Bay, Nelson.

NORTH ISLAND

A Maori song given by Ngata (1970: 102-107) refers to the hakawai flying from Hikitia, Bay of Plenty.

THEORIES FOR THE IDENTITY OF THE HAKAWAI

Although many people tried to catch a glimpse of a hakawai in their torch beam, no-one succeeded. This was easily explained by those who held that the hakawai was a spirit bird (Edwards 1954, Dempsey 1967: 97); it could not be seen anyway. The rest of the muttonbirders disagree as to the size of the hakawai; some insist that it must have been a large bird to make such a loud noise (Billy McQuarrie, pers. comm., Native 1931, Old Timer 1931), whereas others are equally sure that it must have been a small bird to avoid being caught in the torch beam (Claude Skerrett & Rongo Spencer, pers. comm.).

There are several accounts of large birds with multiple wing joints being found around the Stewart Island region, and some people have suggested that these could be the hakawai. Native (1931) mentioned a part skeleton of a bird unearthed at New River Head; one wing was intact and reckoned to be seven feet in length, with nine joints. Beattie (1954: 38) referred to a strange bird washed ashore on Horomamae Island (Fig. 1B) that was mottled and the size of a gannet. The wing spread was disproportionately large, and there were seven joints in the wing. It had a straight, unhooked bill and the wing feathers were 12 to 14 inches in length with rounded tips. On page 36, Beattie claimed that the hakawai was "supposed to be a big, white, land bird with seven joints in its immense wings". Then he mentioned the hokioi of the Tuhoe people "which lived in the sky, flew only by night at a great height, and had four joints in each wing".

The most elaborate description of a hokioi was given to Sir George Grey (1872) by a Maori:

> This bird, the Hokioi, was seen by our ancestors. We (of the present day) have not seen it -- that bird has disappeared now-a-days. The statement of our ancestor was that it was a powerful bird, a very powerful bird. It was a very large hawk. Its resting place was on the top of the mountains; it did not rest on the plains. On the days in which it was on the wing our ancestors saw it; it was not seen every day as its abiding place was in the mountains. Its colour was red and black and white. It was a bird of (black) feathers, tinged with yellow and green; it had a bunch of red feathers on the top of its head. It was a large bird, as large as the Moa.

This is a plausible description of the plumage and behaviour of a large eagle, perhaps *Harpagornis*, an eagle known only from subfossil bones and estimated to have weighed up to 13 kg (R. N. Holdaway, pers. comm.). As far as is known, *Harpagornis* had the normal complement of wing joints.

It is inconceivable that a huge, potentially hominivorous diurnal raptor could remain undetected on a 20 ha island. I suggest that over many generations the eerie call of the unseen hakawai has been linked with racial memories of the most powerful flying bird known to the Maori.

Naturalists from a more prosaic culture have advanced a number of theories to explain the hakawai phenomenon; all but one of the species suggested are seabirds that would come to land only to breed or if storm-driven. Sir Walter Buller and James Cowan favoured the frigatebird (*Fregata* sp.; see Haast 1873 and Beattie 1954: 36). Like the Sooty Tern *(Sterna fuscata)* suggested by Dempsey (1967: 96), the frigatebird can be discounted because it is an infrequent straggler to New Zealand; neither has been recorded in the Stewart Island region.

Neither the Black Petrel *(Procellaria parkinsoni)* suggested by James Drummond (Beattie 1954: 36) and Edgar Stead (Wilson 1959: 148) nor the Shoemaker *(P. aequinoctialis)* suggested in Jenkin (1970: 157) breeds near Stewart Island. Although both species may occur in the seas around Stewart Island, their known calls do not include anything like the hakawai, and they are unlikely to occur over any island on which they do not breed.

Lance Richdale was said to have favoured the Mottled Petrel *(Pterodroma inexpectata)* as the hakawai's alias (Beattie 1954: 36), and Beattie also mentioned the Diving Petrel *(Pelecanoides urinatrix)*. Both these species still breed on many islands around Stewart Island and elsewhere, and their past distributions have always been more extensive than that of the hakawai.

Perrine Moncrieff (1931), in a long letter to the Southland Times, suggested that the call of the hakawai was "likely to be produced by one of the larger shearwaters who are celebrated for the weird noises they make". The only large shearwater known to breed on the islands off Stewart Island is the Sooty Shearwater (muttonbird), which is ruled out of contention by its vast numbers and wide distribution.

The idea that the Stewart Island Snipe might be the hakawai was first suggested in an article in the Southland Times (Anon. 1931). Points in favour of the snipe were that related species overseas had an acoustic aerial display, and that the Stewart Island Snipe had a similar restricted distribution to the hakawai (although the historical distribution of the Stewart Island Snipe has not been investigated in depth previously). However, the hakawai had not been reported from the other New Zealand island groups with snipe: The Snares, Auckland, Antipodes and Chatham Islands (Fig. 1A), and many people considered the flying ability of the Stewart Island Snipe to be inadequate for such a display. Indeed, Guthrie-Smith (1936: 186) considered the Stewart Island Snipe to be flightless.

Moncrieff (1931) argued against snipe being the hakawai from her experience with Common Snipe *(Gallinago gallinago)*. "Surely if the 'Hakawai' were a snipe it would have been located ere now, as snipe make a drumming noise during the breeding season early in the morning, at midday and occasionally on moonlight nights. They are day-birds and would have been observed flying during the daytime". After describing the calls of three Northern Hemisphere snipe species, she concluded that "although peculiar, the noises of the snipe tribe are none of them in the least awe-inspiring or reach the volume of sound attributed to the 'Hakawai' ".

EVIDENCE FOR AERIAL DISPLAYING BY NEW ZEALAND SNIPE

Aerial displays are given by almost all the world's snipes and woodcocks (Tuck 1972, Sutton 1981, Kalchreuter 1982), yet the idea that New Zealand snipe do not have an aerial display is firmly entrenched. The first sentence describing New Zealand snipe in Tuck's monograph (p. 53) states that they "do not have nuptial flights", while *Coenocorypha* is not even mentioned in Sutton's review on aerial and ground displays of the world's snipes.

Evidence for aerial displaying by various forms of New Zealand snipe has accumulated since November 1982, when Don Merton (pers. comm.) heard essentially the same hakawai call on Mangere Island (Chatham Islands) as he had heard on Big South Cape Island in 1961. I studied Chatham Island Snipe on South East and Mangere Islands during November 1983 to January 1984 and in July 1986, and recorded three different kinds of aerial displays. All these displays were performed at night; the most spectacular display included both a vocal and a non-vocal component (Fig. 2A). This display was indeed hair-raising when I first heard it. The vocal component was a disyllabic call, repeated five times, identical to one of the ground diplays given by territorial male Chatham Island Snipe (Fig. 2B). This was followed by a loud roar, similar to a jet passing overhead, as the bird swooped over the 6 m canopy at high speed. The non-vocal component of the call had three stacked bands (0.7 kHz, 0.9 kHz & 1.2 kHz) and lasted for about 1.5 seconds.

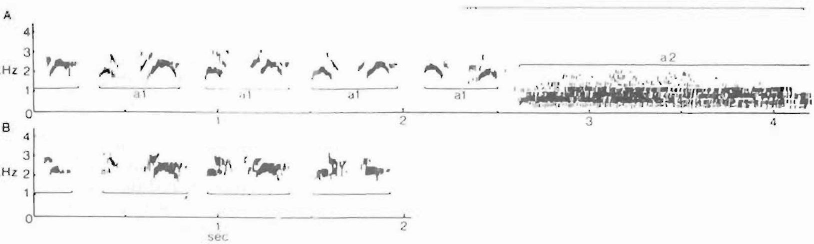

FIGURE 2 — Sonographs of displays by Chatham Island Snipe, recorded on South East Island, c.2330 h on 9 January 1984. The first syllable of both calls was not recorded. The two calls were given by different birds.
A. Aerial display, showing a series of five disyllabic vocal phrases (a1) followed by a non-vocal 'roar' (a2).
B. Ground display given by a male, showing the same song structure as in 'a1'.

As yet no-one has managed to see a Chatham Island Snipe perform the display, but high-flying snipe have been seen in spotlight beams on nights when birds have been displaying, and I have seen snipe performing a separate, purely vocal aerial display.

If this aerial display of Chatham Island Snipe is homologous with the 'drumming' or 'bleating' of *Gallinago* snipes, the non-vocal part of the call is likely to be created by air currents making the tail feathers vibrate as the bird dives at speed. I found indirect evidence of this on two of the 24 adult male snipe that I handled on South East Island in November 1983-January 1984. Their tail feathers had unusual wear. The shafts of all 14 rectrices had snapped off about 5 mm from the tip, creating a V at the tip of each feather. I attribute this unusual feather wear to vibrational stress during the display. Other snipe species show tail wear caused by their aerial displays; male Wilson's Snipe *(G. gallinago delicata)* can be distinguished during the breeding season by their frayed tail feathers (Tuck 1972: 167, and see frontispiece in Sutton 1981).

The unusual wear of tail feathers described above can also be seen in museum specimens (Fig. 3). At least ten snipe skins in New Zealand museums show such wear: three or four from the Chatham Is, two from islands off Stewart I., four or five from the Auckland Is and one from Antipodes I. (Table 2). Table 3 gives how often I found tail wear among New Zealand snipe, separated by sex and by island group. As feather wear would be most pronounced before moult and specimens have been collected or handled throughout the year, I can draw little conclusion from tail-feather wear about the frequency of aerial displaying by the different snipe taxa. Note two points, however: this form of tail wear is found mainly in male snipe; and there is no evidence for such tail wear in Snares Island Snipe *(C. a. huegeli)*.

The only evidence to date for aerial displaying by Auckland Island Snipe *(C. a. aucklandica)* is tail-feather wear in the four or five specimens given in Table 2, but I have since received corroborating evidence for aerial displaying by Antipodes Island Snipe *(C. a. meinertzhagenae)*. D. S. Horning (pers. comm.), who was on Antipodes I. in December 1978, writes:

> The bird was heard at dawn (before the sun came over the horizon) on Monday, 4 December 1978. I was sitting on some tussock at the cliff edge . . . [and witnessed] a snipe (from 20 m or so) diving. I took notice of it because I had not seen this behaviour at The Snares. It dived only three times that I saw – a very steep dive but not straight down. The bird did not make any calling sounds that I could hear and there was a wing rustle at the bottom of the dive. It then disappeared into the tussock and flew into the air again [about] 3-4 minutes later, repeating the dive. There was another bird involved, but I could not say [that] only one bird did the diving . . .

It is ironic that the most intensively studied population of New Zealand snipe – that on The Snares – is the only population for which there is no evidence for this form of aerial display. I have handled adult snipe 577 times on The Snares during 15 months of field work between December 1982 and February 1987 and have yet to hear the display or notice the characteristic tail-feather wear. I have, however, morphological and behavioural evidence that Snares Island Snipe have less flying ability than other New Zealand snipe.

WAS THE STEWART ISLAND SNIPE THE HAKAWAI?

Given the apparent extinction of both Stewart Island Snipe and hakawai, and the absence of tape-recordings of hakawai, it is not possible to test directly the hypothesis that the hakawai was the Stewart Island Snipe giving an aerial display. However, two avenues for investigation remain open: how do the geographical and historical distributions of hakawai and snipe compare, and how similar is the aerial display of the Chatham Island Snipe to human recollections of the hakawai?

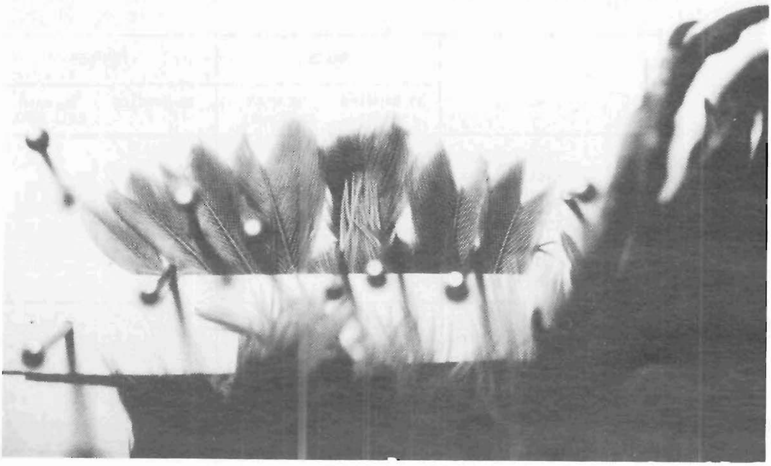

FIGURE 3 — Tail-feather wear in male Chatham Island Snipe (NMNZ DM 720) attributed to aerial displaying. The shafts of the rectrices have snapped near the tip.

TABLE 2 — New Zealand snipe specimens in New Zealand museums that show tail-feather wear attributed to aerial displaying. AIM = Auckland Institute & Museum; CM = Canterbury Museum; NMNZ = National Museum; OM = Otago Museum. AIM AV 77.4 and 78.9 may have suffered feather damage for reasons other than aerial displaying. OM A 07 101 seems to be incorrectly sexed.

Chatham Island Snipe (*Coenocorypha pusilla*)	CM AV 1804	♂	South East I.	[Dannefaerd/O'Connor]
	CM AV 2757	♂	Chatham Is	[O'Connor collection]
	NMNZ DM 720	♂	South East I.	1939
	AIM AV 78.9	♂	Chatham Is	[Dannefaerd]
Stewart Island Snipe (*C. aucklandica iredalei*)	CM AV 729	♂	"?Jackie Lees/Solomon"	[Stead collection]
	CM AV 732	♂	"?Jackie Lees/Solomon"	[Stead collection]
Auckland Island Snipe (*C. a. aucklandica*)	NMNZ DM 17515	♂	Adams I.	3 Jan 1973
	NMNZ DM 17516	♂	Adams I.	30 Dec 1972
	NMNZ DM 17517	♂	Adams I.	30 Dec 1972
	OM A 07 101	"♀"	Auckland Is	March 1907
	AIM AV 77.4	-	[no data, poor condition]	
Antipodes Island Snipe (*C. a. meinertzhagenae*)	NMNZ DM 14538	♂	Antipodes I.	4 Feb 1969

TABLE 3 — The frequency of tail-feather wear attributed to aerial displaying found in New Zealand snipe

		MALES		FEMALES	
		No. handled	No. with tail wear	No. handled	No. with tail wear
C. pusilla	live (South East I.)	36	2	39	1
	museum skins	36	3(?4)	36	0
	TOTAL	72	5(?6)	75	1
C. a. iredalei	museum skins	4	2	3	0
C. a. huegeli	live	320	0	257	0
	museum skins	7	0	6	0
	TOTAL	327	0	263	0
C. a. aucklandica	museum skins	7	3(?4)	15	(?1)
C. a. meinertzhagenae	museum skins	5	1	4	0

I. HISTORICAL DISTRIBUTION OF SNIPE ON MAINLAND NEW ZEALAND AND ADJACENT ISLANDS

The only islands from which there are documented skins of Stewart Island Snipe are Jacky Lee I., where Travers collected the type specimens of *C. a. iredalei* in 1897, and Big South Cape I. (two skins in NMNZ collected September 1964). Six skins collected by E. F. Stead and held at Canterbury Museum are labelled "? Jacques Lees/Solomon". These skins are probably from Big South Cape I., as there is no record of Stead finding snipe on Jacky Lee or Solomon Is (Stead 1932, Wilson 1959); Stead collected eight eggs of *C. a. iredalei*, now in Canterbury Museum, on Big South Cape I. in December 1931.

Guthrie-Smith was deliberately vague when describing where he had seen snipe. In 1936 he wrote (p. 175) ". . . I knew [snipe] to be resident on many of the small islands east of Half Moon Bay; I had seen specimens of them on former expeditions", yet he does not mention snipe in his 1914 book describing his experiences on Herekopare, North and 'neighbouring' islands.

The distribution of Stewart Island Snipe, South Island Snipe (*C. a.* subsp.) and North Island Snipe *(C. a. ?barrierensis)* given below was composed from the scant information in the literature, conversations and correspondence with muttonbirders, and from subfossil remains held in New Zealand museums. Refer to Fig. 1 for the location of the various islands.

A. The islands off the south-west coast of Stewart Island

Big South Cape Island

The last official record of Stewart Island Snipe was of two birds captured by NZ Wildlife Service staff on Big South Cape I. on 30 August 1964 (Bell, B. D., Southern islands bird transfer expedition, August-September 1964. Unpubl. report NZ Wildlife Service) during a bid to save vulnerable bird species from a plague of ship rats. These two birds died before they could be moved to another island and are now in the National Museum. Two muttonbirders have reported sightings of snipe on Big South Cape I. in 1965, 1978 and 1984.

Guthrie-Smith (1936: 181) saw snipe on Big South Cape I. (which he called by the fictitious name Kaipara) during an hour ashore in late December 1913. The snipe were in "the woodlands" (i.e. near the coast) and Guthrie-Smith was not aware of weka being present. In November 1923 weka were plentiful , apparently having been liberated during the ensuing decade (Guthrie-Smith 1936: 182). Snipe were found only on the heights and burnt-out centre of the island, whereas weka were confined to "the fertile bush and luxurious undergrowth" of the coastal fringe.

Stead and Wilson saw snipe "above the bush line" on Big South Cape I. in December 1931 (Wilson 1959: 49) and found "a good number" of weka. Richdale (no date a) found few weka and few snipe in January 1945, but did see one weka well above the bushline. Bell & Merton (unpubl.) saw only one snipe during a month's stay in April 1961.

Solomon Island

Wilson (1979: 81) and Bell (1978) recorded snipe as formerly occurring on Solomon I. Bell misquoted Guthrie-Smith (1925), who did not mention seeing snipe on Solomon I. (for which he invented the name Kotiwhenu). Guthrie-Smith in 1913 and Stead and Wilson in 1931 had to travel across to Big South Cape I. from Solomon I. to view snipe.

Pukeweka

Pukeweka is a small islet (c. 1.5 ha) lying between Solomon and Big South Cape Is. Phillip Smith (pers. comm.) had seen snipe on Big South Cape I and Pukeweka before the rat plague. Pukeweka has been suggested as the site where ship rats got ashore in the South Cape group, before spreading to neighbouring Big South Cape and Solomon Is in 1963.

Little Moggy Island (Moki-iti)

Patu King (pers. comm.) reports having seen snipe on Little Moggy Island, which lies 500 m north-east of Big Moggy I., and he suspects that they could still be there. Little Moggy I. is thought to be rodent free, but weka were "plentiful" in March 1965 (Blackburn 1965). Snipe were not seen in March 1965 (B. D. Bell, pers. comm.).

Kundy Island

Oliver (1930) and Richdale (no date b) gave Kundy as one of the islands where snipe occurred, although Oliver (1955) excluded this locality without comment from the second edition of *New Zealand Birds*. Neither author indicated the source of the record. Stead and Wilson visited Kundy I. for a month in November 1929 (some 18 years before weka were introduced – R. Trow, pers. comm.) but did not record snipe. Russel Trow, whose family have been muttonbirding on Kundy I. since 1905, was not aware of snipe having been there.

B. Solander Islands

Falla (1948) heard a "snipe-like call" on unmodified Little Solander Island during a brief landing on 20 July 1948. I found no evidence of snipe during two days on the island in July 1985 (Cooper *et al.* 1986).

C. The islands off the north-east coast of Stewart Island and in Foveaux Strait

Herekopare Island

Harold Ashwell and Alan Skerrett both told me of the former occurrence of snipe on Herekopare Island, although the three people who had heard hakawai on Herekopare could not recall seeing snipe there. Snipe are presumed to have died out in the mid-1920s after cats were introduced and weka reintroduced.

It is possible that Guthrie-Smith saw snipe on Herekopare and/or Jacky Lee Is in 1911, as he stated that he had seen snipe on islands off Half Moon Bay (1936: 175). The absence of references to snipe in *Mutton Birds and Other Birds* (1914) may be part of the deception intended by the use of the fictitious names Kaipara and Kotiwhenu for Big South Cape and Solomon Is. While Guthrie-Smith's motive for deception – to protect the birds and islands from those who would exploit them – is beyond reproach, the net result 70 years later is an unnecessary knot in the tangle of intrigue surrounding snipe and hakawai.

Jacky Lee Island

I presume weka were absent from Jacky Lee Island when H. H. Travers collected snipe there in March and October 1897 and April 1901. Muttonbirding ceased in 1929, three years before the visit by Stead and Wilson (Wilson 1959: 59). Weka were "very plentiful" in December 1932. Wilson (p.60) wrote: "We found no trace of the snipe which had been reported from the Jacques Lees; but from the number of wekas we saw and their predatory habits it was evident that, if snipe had inhabited the island, they could not have survived long after the wekas had arrived". Eight years later weka numbers had "increased tremendously" and had decimated Diving Petrel and prion populations (Wilson 1959: 101-102).

Ruapuke Island

Billy McQuarrie informed me of old reports of snipe on Ruapuke Island; this is confirmed by subfossil remains in the Canterbury Museum.

Native Island

This small island is in Paterson Inlet (Fig. 1C). A part clavicle of *Coenocorypha* from a 'moa-hunter midden' on Native Island is in the Canterbury Museum.

D. The main islands of New Zealand

Stewart Island

Subfossil remains of snipe collected at The Neck (southern entrance of Paterson Inlet) are in Canterbury Museum.

South Island

Bones of *Coenocorypha* have been found in dune deposits at Marfell's Beach, Marlborough (Scarlett 1979) and in caves near Karamea, Punakaiki, Waipara, Timaru and Te Anau. Given the distribution and degree of subspeciation of *C. aucklandica*, it is likely that the South Island held a distinct subspecies. However, the presumed range of *C. a. iredalei* reached within 12 km of the South Island coast (at Ruapuke I.). Unless consistent differences are found between bones of South Island and Stewart Island Snipe, I suggest that all should be referred to *C. a. iredalei*.

North Island

On 30 August 1820 Major Richard Cruise shot a snipe on Motukorea Island (Browns I.) in Hauraki Gulf. He wrote (Cruise 1823: 225): "[the snipe was] the only one that any of us had seen in this country: in its plumage it resembled those found in England, but the bird itself was much smaller". The only existing snipe skin from the North Island region was taken on Little Barrier Island (Hauraki Gulf) in 1870 (Hutton 1871; see discussion in Turbott 1961). Although this unique specimen was named the Little Barrier Snipe *(C. a. barrierensis)* by Oliver (1955), Little Barrier I. was probably merely the final refuge of the North Island Snipe, which is known from subfossil deposits in the King Country, Hawke's Bay and Wairarapa (Medway 1971, Paulin 1973, Milliner 1981, Horn 1983). Thus, North Island records of *Coenocorypha* should be referred to *C. a. barrierensis* in the absence of evidence to the contrary.

Table 4 compares the historical distributions of snipe and hakawai around mainland New Zealand and offshore island groups. Given the uncertainties of the data set, both geographical distribution and the decline over time agree surprisingly well between snipe and hakawai. Snipe were known from five of the seven acceptable 'hakawai' islands off Stewart Island, and hakawai were known from five of the six 'snipe' islands. On most islands the decline of the hakawai is better known than that of snipe, probably because observers took more notice of hearing the hakawai. The isolated records of hakawai from Kundy and Big Moggy Is suggest that there was some movement between islands.

On Big South Cape I. even the habitat preference of snipe and hakawai agree (at least after the introduction of weka), both being found in the central pakihi areas of the island.

II. RESPONSE TO TAPE OF AERIAL DISPLAY OF CHATHAM ISLAND SNIPE

On playing a tape recording of the aerial display of Chatham Island Snipe represented in Fig. 2A, I had a response from ten people who had heard the hakawai in the previous 20-60 years. Seven of the observers had heard the hakawai on Big South Cape I. as recently as the early 1960s, and three had last heard it on Herekopare I. in the 1920s.

Four people (including B. D. Bell and D. V. Merton of the NZ Wildlife Service) thought the tape to be a fair representation of the hakawai's call. The three others from Big South Cape I. did not think that the tape was the hakawai, but considered it the nearest likeness to the call of the hakawai that they had heard. Differences stressed (independently) were that the vocal component *hakwai, hakwai . . .* was too high pitched and "not human enough" on the tape. All three said that the non-vocal 'roar' reminded them of the hakawai. Note that none of these first seven considered the hakawai to sound like a chain rattle.

The three observers from Herekopare did not recognise the tape recording, and again stressed the human-like sound of the bird calling out its name. Two emphasised the chain rattle description for the non-vocal component. It is a shame that none of these people had heard the hakawai on Big South Cape I. Did the call differ from island to island, or was I expecting too much from recollections of 60 years ago?

TABLE 4 — The distribution and decline of hakawai and snipe on the main islands of New Zealand and adjacent offshore islands. Islands given in bold type are considered to have held hakawai and/or snipe in the last 100 years. See text for authenticity of records.

Locality	Approximate date of disappearance	
	Hakawai	Snipe
Big South Cape	1960s (possibly surviving)	1960s (possibly surviving)
Pukeweka	——	1960s
Solomon	1930s	?1930s (irregular)
Poutama	1930s	——
? Kundy	?1920s	?1920s
? Little Moggy	——	possibly surviving
? Big Moggy	?1940s	——
? Little Solander	after 1950	after 1960
Jacky Lee	1920s	1920s
Herekopare	1920s	1920s
Ruapuke	late 1800s	late 1800s
Green	late 1800s	——
Native	——	subfossil
Stewart Island	?late 1800s	subfossil
South Island	late 1800s (southern coast)	subfossil
Little Barrier	——	1870s
Motukorea	——	1820s
North Island	pre-1800 (Bay of Plenty)	subfossil

CONCLUSION

Many pieces of the hakawai puzzle are missing, probably forever, and other pieces have been shoe-horned into place, but all the available evidence indicates that the hakawai of the southern muttonbird islands was an aerial display of Stewart Island Snipe. Further north, away from the last refuge of 'mainland' snipe, memories of the awe-inspiring nocturnal call of the unseen hakawai appear to have been blended with traditional recollections of a fearsome diurnal presence, perhaps the extinct eagle *Harpagornis*.

Some of the differences described between the call of the hakawai and the tape recording of an aerial display of the Chatham Island Snipe may be due to differences in body size. The Stewart Island Snipe is estimated to have weighed 30% more than the Chatham Island Snipe (mean male bodyweight 76 g; Fig. 4), and so its call may have had a lower pitch. Territory calls given from the ground by Chatham Island Snipe are markedly higher pitched than homologous calls given by Snares Island Snipe (mean male bodyweight 103.5 g).

FIGURE 4 — Male Chatham Island Snipe — the unpretentious source of a legend?

The characteristic tail-feather wear described for New Zealand snipe is, in my opinion, caused by vibrational stress during aerial display. Non-vocal acoustic displays produced by flight feathers are known for two New Zealand honeyeaters (Craig 1984 & 1985, Onley 1986). Structural modifications to the outer primaries of Tui *(Prosthemadera novaeseelandiae)* and Bellbirds *(Anthornis melanura)* are thought to be the cause of whirring produced in flight; whereas modification to snipe rectrices is thought to result from their aerial display. If the amount of wear affects the quality of sound produced during the display, this may account for different descriptions of the non-vocal component of the hakawai's call.

If we can accept that the hakawai was a nocturnal display of Stewart Island Snipe, our knowledge of the recent distribution of the snipe is extended. Islands thought to have held Stewart Island Snipe in the last 100 years are Big South Cape, Pukeweka, Solomon, Poutama, Jacky Lee, Herekopare, Ruapuke and Green Is. Isolated records of hakawai from Kundy and Big Moggy Is suggest that there was some movement between islands. The disappearance of snipe from these islands can be attributed to ship rats (Big South Cape and Pukeweka Is), weka (Solomon, Poutama, Jacky Lee and Green Is) and a combination of weka and cats (Herekopare and probably Ruapuke Is). What about those islands which, from their size, location and vegetation, should have held snipe, but from which there are no records: Putauhinu, Codfish, Edwards and Bench Is? Putauhinu has had kiore and cats, Codfish I. has kiore and weka, Edwards I. has weka, and Bench I. has Norway rats and weka. The inference is that Stewart Island Snipe cannot last in the presence of cats or any species of rat and may be wiped out by weka. The successful reintroduction of Chatham Island Snipe to Mangere Island by the NZ Wildlife Service in 1970 and 1972 adds support to these conclusions; snipe had disappeared after cats were introduced in the 1890s (the cats had died out by 1960). That snipe survived on Big South Cape I. in the presence of weka could be explained by the large size of the island, the diversity of habitats, and the very effective control of the weka by muttonbirders. These conclusions place severe constraints on what islands can be used for relocating snipe.

ACKNOWLEDGEMENTS

I am grateful to Don Merton for drawing my attention to aerial displaying by Chatham Island Snipe, willingly supplying field notes, and allowing access to NZ Wildlife Service files. This paper owes much of its content to the muttonbirders; I thank the following people for our enjoyable conversations and correspondence about the hakawai: Harold Ashwell, Noki Barrett, Jimmy Bull, Jack Hart, Patu King, Marty McColgan, Jack McKay, Billy McQuarrie, Olaf Nilsen, Nash Norton, Alfie Ryan, Alan Skerrett, Claude Skerrett, Phillip Smith, Russell Smith, Rongo Spencer, Russel Trow and Eileen & Buddy Willa. Further information was supplied by Brian Bell, Don Horning and Ronald Lockley. Thanks also to Wynston & Lorraine Cooper, Ian & Mary Leask, Joe Murphy, and Murray & Nancy Schofield for their hospitality during my stays in Invercargill, Bluff, and Stewart Island.

Mike Nepia translated some of the Maori passages quoted, and Joe Waas assisted with sonograph preparation. The manuscript was improved by comments from Barrie Heather, Ian McLean, Don Merton, Bill Nepia, Paul Sagar and Dick Sibson.

I have received financial assistance towards my snipe research from Department of Lands & Survey and Royal Forest & Bird Protection Society.

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Printed by TE RAU PRESS LTD., Peel Street, Gisborne

Appendix 2

Breeding ecology of Snares Island and Chatham Island Snipes.

Abstract

Snares Island Snipe (*Coenocorypha aucklandica huegeli*) were studied on the Snares Islands during parts of six breeding seasons between 1982 and 1987. Laying occurred between 4 November and 19 February; the breeding season (including chick-rearing) spanned the months November to May. Nests were well concealed among dense vegetation with solid overhead cover (e.g. branches or fern trunks); 33 nests (73%) were simple scrapes in detritus under fern clumps; 12 nests (27%) were well-formed cups of grass or sedge leaves among a tussock or sedge clump. Most matings were monogamous, with shared incubation of the two-egg clutch. Spot-checks at 32 nests revealed that males incubated for 51% of the time, mainly at night and during late afternoon. Females were on nests 49% of the time, mainly during the morning and early afternoon. The eggs hatched synchronously and the chicks stayed in the nest for less than 13 h. The male cared for the first chick to leave the nest. Development of chicks is described using Gompertz growth equations. Full juvenile plumage took about 54 days to attain. Full adult size in all growth parameters was attained soon after independence (c.65 days).

Chatham Island Snipe (*C. pusilla*) were studied on Rangatira Island during the 1983-84 breeding season. Laying was estimated to extend from September to January. Most nests found (86%) were under *Carex* sedges. Incubation of the two-egg clutch was shared, but incubation patterns were not determined. The eggs were 19% smaller in relation to predicted egg-weight than those of Snares Island Snipe. The eggs hatched synchronously and the chicks stayed in the nest for less than 11.5 h. The male cared for the first chick to leave the nest. Full juvenile plumage took about 47 days to attain. The bill grew much more rapidly than for Snares Island Snipe and chicks became independent much earlier (c.41 days old).

Introduction

New Zealand snipes (*Coenocorypha* spp.) are among the least studied of New Zealand's endemic birds. Local extinctions have confined these snipes to islands that do not have introduced predators (Appendices 1 & 3). On these islands, snipe occur at high densities in the absence of effective predators or foraging competitors (Chapters 1 & 3), occupying tussock grasslands, megaherb gardens, scrub, forest and areas of sedge. Our limited knowledge of the life histories of *Coenocorypha* snipes is due to the remoteness of the islands, their dense vegetation, and the secretive behaviour of snipe (Stead 1948, Warham & Bell 1979, Appendix 1). Only the Snares Island Snipe (*C. aucklandica huegeli*) and Chatham Island Snipe (*C. pusilla*) have been studied enough for their behaviour and ecology to be compared (e.g. Chapter 1, Appendices 1 & 4).

Chatham Island Snipe are about 30% smaller than Snares Island Snipe (Chapter 1) and have lower wing-loadings and greater flying ability (Appendix 4). Recently, I summarised features of the breeding systems of Snares Island and Chatham Island Snipes that I considered had arisen due to severe food limitation during the breeding season (Chapter 1). Compared with Common Snipe (*Gallinago gallinago*), *Coenocorypha* snipes occurred at high densities and had courtship feeding, large eggs, a long egg interval, a small clutch and shared incubation. Hatching success was high, but chick growth rates were slow and there was a long period of chick dependence (Chapter 1).

In this paper I describe breeding seasons, nests, eggs and chick development of Snares Island and Chatham Island snipes, and the roles of the sexes during nest site selection, incubation and hatching. This information should be of use in designing captive-rearing programmes for snipe and as a baseline for comparative studies of Auckland Island Snipe (*C. a. aucklandica*) and Antipodes Island Snipe (*C. a. meinertzhagenae*).

Study areas and methods

Snares Island Snipe were studied during seven expeditions to the Snares Islands (48°02'S 166°36'E) between December 1982 and December 1987. Fieldwork of 477 days, spanning September to March, included parts of six breeding seasons. The 7.5 ha study area of *Olearia lyalli* forest held about 20 pairs of snipe, all of which I individually colour-banded. I found nests by tracing the source of calls (n = 20), systematic searching (n = 19), chance disturbance of incubating adults (n = 4), or following returning adults (n = 2). Detailed descriptions were taken for 36 nests. Eggs were measured to 0.1 mm with vernier calipers.

Nests were checked daily, or more frequently during laying and hatching. Hides were erected at four nests and five 24-h observations of incubation patterns were undertaken in the middle of the incubation period. A chart recorder, light beams and photo-electric cells installed at one nest gave a trace showing activity during laying of the second egg. If a bird sat on the nest the two light beams were broken, activating an ink pen on a revolving drum. The pen returned to base level when the bird left the nest and the light beams were uninterrupted. First-egg laying dates for 25 nests were calculated from hatching dates by subtracting 22 days for incubation and three days for egg interval (Chapter 1).

Each of 35 known-age chicks was captured 4.6 ± 5.0 times (range 1 - 18 times) between hatching and age 78 days (total = 160 handlings) and standard measurements taken. Linear measurements were recorded to 0.1 mm and weights to 0.1 g. Patterns of growth were found to conform most closely to the Gompertz equation, as in other Charadriiformes (Ricklefs 1973, Green 1985). Gompertz curves were fitted to chick growth parameters using the Maximum Likelihood Program (Ross 1980); the equations were of the form:

$$Y = A + C \times \exp(-\exp(-D(T - M)))$$

where Y is the measured parameter, T is the age in days, and A, C, D and M are constants. The asymptote of the curve is equal to $A + C$. Growth constants ($K_G = e \times dY/dT$ at the point of inflection; Ricklefs 1967) for weight and culmen-length were obtained by preparing the data as proportions of the asymptote, and then solving Equation 2:

$$dY/dT = B \times C \times \exp(-\exp(-B(T - M) + B(M - T)))$$

at the point $Y = 1/e$. Growth rates of known-age chicks were used to calculate hatching dates for 38 chicks of unknown age. Thus, hatching and laying dates were calculated for all 58 breeding attempts recorded in the study area over five breeding seasons.

Chatham Island Snipe were studied on Rangatira (South East) Island (44°21'S 176°10'W), 25 November 1983 to 18 January 1984. The 4.3 ha study area of *Olearia traversi* and *Plagianthus regius* forest contained about 24 snipe territories. Observation techniques were similar to those outlined for Snares Island Snipe.

Fourteen nests were found by systematic searching, and 28 eggs measured. Laying dates were estimated from hatching dates by assuming that incubation length and egg interval were similar to those for Snares Island Snipe. Each of 28 known-age chicks was captured 2.4 ± 1.4 times (range 1 - 4) between hatching and age 89 days (total = 66 handlings). Gompertz curves were fitted to chick growth parameters, and growth constants for weight and culmen-length calculated using Equation 2.

Hatching dates for 21 chicks of unknown age were estimated by comparing development with growth rates of known-age chicks, allowing hatching and laying dates to be estimated for all 40 breeding attempts recorded within and around the study area.

Measurements are given as mean ± s.d., with range in parentheses, unless otherwise stated.

Results and discussion

Breeding season

Snares Island Snipe: The date of the first egg laid over five breeding seasons ranged from 4 to 28 November (mean 16 November). The last egg in three breeding seasons was laid between 7 and 19 February (mean 12 February). Laying during these three breeding seasons extended over 79 ± 9 days (71 - 89 days). As incubation and chick-rearing took about 87 days (Chapter 1), the breeding season on the Snares Is typically extended from mid-November to mid-May. Horning & Horning (1974) saw a small downy chick on 4 May 1972, which must have hatched from a clutch laid in early April. However, as no other small chicks had been seen for several months, this record was considered exceptional (D.S. Horning pers. comm.).

Chatham Island Snipe: Laying in 1983 was estimated to have extended from 23 September to 29 December. Ignoring possible failed early nests, laying extended over 97 days, and was almost two months earlier than for Snares Island Snipe. As incubation and chick-rearing took about 63 days (Chapter 1), the 1983-84 breeding season was estimated to have extended from late September to the end of February. Laying occurred earlier in 1981; Mike Dennison (*in litt.*) saw a small chick on Mangere Island on 28 September that must have hatched from an egg laid in the first week of September. The latest breeding record is of a bird sitting on two eggs on 5 February 1985, Rangatira Island (Gaze 1986); if these eggs were fertile, they must have been laid after 14 January.

Laying by snipe on the Snares Islands coincided with an annual peak in prey abundance between late November and early February (Chapter 5). The much earlier laying season of Chatham Island Snipe suggests that peak prey abundance was two months earlier on the Chatham Islands.

Mating system

Snares Island Snipe: About 95% of matings at the beginning of the breeding season were monogamous; the remaining 5% were cases of simultaneous polygyny (Chapter 1). Monogamous pairs shared incubation at the same nest (described below). Details of female single sex incubation (associated with simultaneous polygyny) were given in Chapter 2.
Chatham Island Snipe: All matings seen were monogamous, but the sample (10 nests) was too small for rare mating strategies to be noticeable.

Nest sites

Nest sites were chosen by courting pairs, but only females were seen to construct nests (although, incubating males rearranged nest materials). Nests were constructed from materials within reach of the nest, except for two nests where *Poa* leaves had been carried at least 1 - 1.5 m.
Snares Island Snipe: They made two types of nest depending on the site chosen. Type I (Fig. 7.1a) nests were in fern clumps (n = 33, 73% of nests found). Most (n = 24) were on the downhill side of clumps of prickly shield fern (*Polystichum vestitum*), with the nest sheltered above by a solid *Polystichum* trunk and at the sides by the skirt of dead fronds. The remaining nine Type I nests were in clumps of shore spleenwort (*Asplenium obtusatum*) and/or coastal hard fern (*Blechnum durum*). Type I nests were formed from plant detritus that had gathered under the skirt - generally fern fragments but also tree leaves and fragments of bark. The eggs were laid in a shallow natural depression, if there was little detritus, or in a bowl up to 6 cm deep. Mean bowl depth for 24 Type I nests was 1.8 ± 1.8 cm. The internal diameter of 23 nests was 10.0 ± 1.4 cm (8.5 - 13 cm). Of the 33 Type I nests, 32 had solid wood or matted stipes 18.6 ± 5.4 cm (10 - 30 cm) above the bowl.

Type II nests (Fig. 7.1b) were found in the heart of *Carex trifida* sedges (n = 9) or *Poa tennantiana* tussocks (n = 3). A Type II nest has also been found in a *Poa astonii* tussock (P.M. Sagar *in litt.*). Nests were well-formed cups constructed of substantial amounts of *Carex* or *Poa* leaves. Mean cup depth of 10 nests was 4.0 ± 2.4 cm (1 - 10 cm). The internal diameter of the cup was 11.1 ± 1.3 cm (9 - 13 cm). Of the 12 Type II nests, eight had solid wood 18.6 ± 8.9 cm (7 - 30 cm) above the cup. The remaining four nests were protected above by a dense crown of sedge or tussock leaves.

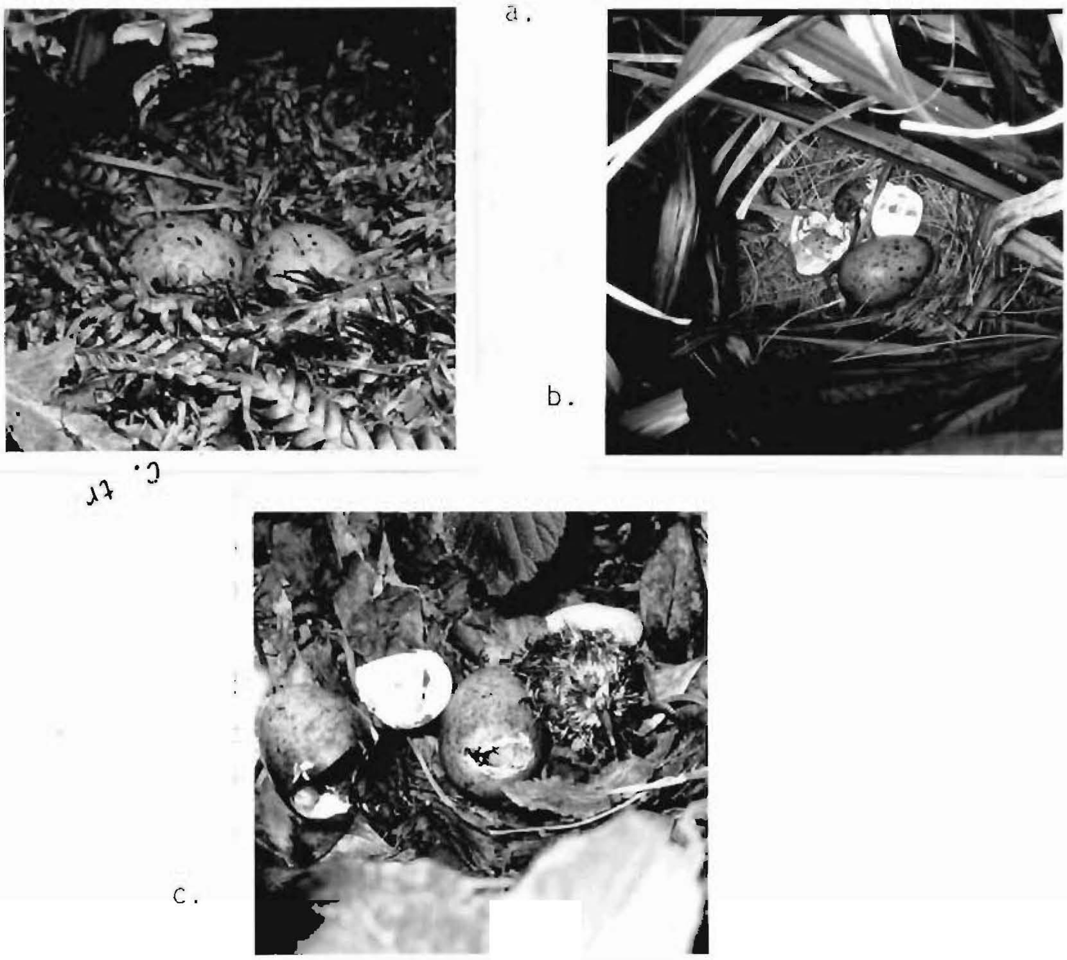

Figure 7.1.a. Snares Island Snipe Type I nest under *Polystichum vestitum* fern. A simple scrape in detritus, surrounded by fern fronds.
7.1.b. Snares Island Snipe Type II nest under *Carex trifida* sedge. A well formed cup of *Poa astonii* and *Carex* leaves.
7.1.c. Hatching Chatham Island Snipe in nest under blackberry. This nest was unlined, but 86% of nests were lined with sedge or grass leaves.

Of eight females for which 2 - 5 nests each were found, four constructed only Type I nests (n = 14 nests) and four constructed both types of nest (6 x Type I, 7 x Type II). The choice of nest site (and type) seemed to depend on what sites were available - those females whose mate's territory did not contain extensive areas of *Poa* or *Carex* constructed only Type I nests.

Empty scrapes were often found during systematic searches, and so snipe may make more than one nest before laying. This was confirmed in the following case. Two empty nests were found 2 m apart on 25 November 1987. The resident female was seen within 3 m of these nests on four occasions over the next five days (the male was never seen near the nests). Small amounts of detritus placed daily in the nests were removed or incorporated into the nest. On 30 November, the female was sitting on Nest B at 0840 hrs, and on Nest A at 1450 hrs. An egg was laid in Nest A between 1450 and 1605 hrs.

Three nest sites were used more than once. One site was used in three different seasons by three different pairs. The second site was used in two consecutive seasons by the same male with different females. The third site was used in the same season by the same male with two consecutive mates (his first mate had used a second site before the male returned to the first site with his second mate). No female was found to reuse a nest site.

Chatham Island Snipe: 12 of the 14 nests found were under *ifida*, one was under blackberry (*Rubus fruticosus*; Fig. 7.1c) and one was under Yorkshire fog grass (*Holcus lanatus*) and bracken (*Pteridium esculentum*). Nests were shallow cups of *Carex* or *Holcus* leaves (n = 12) or simple unlined scrapes (n = 2; Fig. 7.1c).

A major cause of nest loss for passerines on the Snares Is and Rangatira I. is damage by 'crash-landing' petrels (Cemmick & Veitch 1985, McLean & Miskelly 1988, pers. obs.). Sooty Shearwaters (*Puffinus griseus*, mean adult body-weight 819 g) breed at an average density of 11 600 pairs/ha under *Olearia* forest on the Snares Is (Warham & Wilson 1982). Snipe nests on the Snares Is were all well protected above by solid wood or matted vegetation or were in areas with a very dense *Olearia* canopy. Chatham Island Snipe nests on Rangatira I. were less well protected, often under small *Carex* sedges in clearings or at forest margins. The predominant petrel species breeding on Rangatira I. (White-faced Storm Petrel *Pelagodroma marina*, 55 g; Broad-billed Prion *Pachyptila vittata*, 202 g) are much lighter and land more gently than Sooty Shearwaters. Thus, the weight and landing habits of locally abundant nesting petrels may influence nest sites chosen by *Coenocorypha* snipes.

Laying

I determined laying time within six hours for nine Snares Island Snipe eggs. Eight were laid between 0910 hrs and 2050 hrs (mean 1458 hrs ± 2 h 55 min), the ninth was laid during the night. The two eggs in each clutch were laid three days apart (n = 5; Chapter 1).

Activity at one nest was followed in detail for 8 h 20 min until the second egg was laid (Fig. 7.2). A bird visited the nest briefly 6 h 07 min, 4 h 55 min and 3 h 50 min before the egg was laid. The female was on the nest continuously for 2 h 06 min until the egg was laid, with much vigorous movement during the last 1 h 18 min. Steady incubation began as soon as the second egg was laid.

I have no information on laying for Chatham Island Snipe.

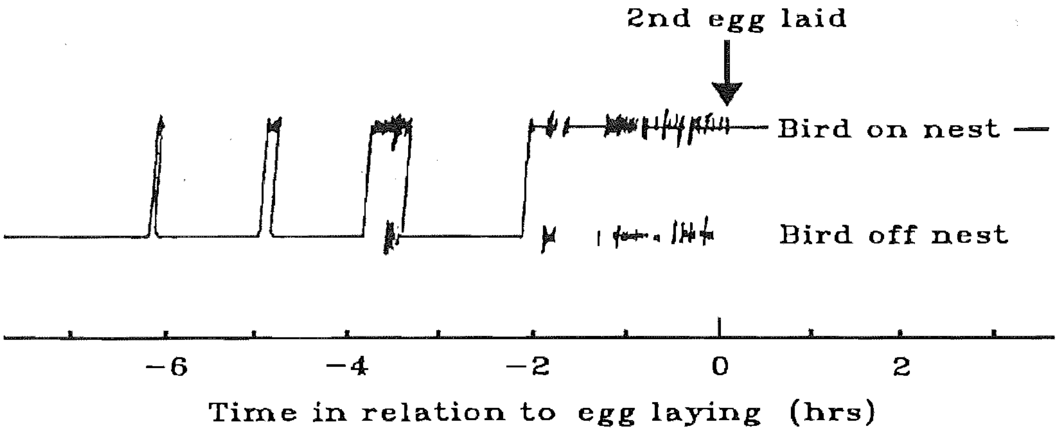

Figure 7.2. Activity at a Snares Island Snipe nest during the $7^1/_2$ hours before laying of the second (final) egg. The tracing was obtained using an activity recorder (see Methods). A blurred trace is caused by frequent movement of a bird at the nest; a smooth trace indicates inactivity.

Eggs

Snares Island Snipe: The eggs were bluntly ovoid, light to very pale brown, and marked with dark brown, pale brown and mid-grey spots and blotches, especially around the larger end. Length was 43.9 ± 1.1 mm (39.1 - 46.4 mm, n = 81) and width was 31.9 ± 0.6 mm (30.4 - 33.1 mm, n = 81). Fresh weight was estimated as 23.7 ± 1.1 g (21.1 - 26.7 g, n = 81; Chapter 1). Estimated egg-weight loss during incubation was 15.9 ± 2.3% of fresh weight (n = 40).

Chatham Island Snipe: The eggs were pale pinkish brown, marked with fine spots of dark brown and larger blotches of mid-grey around the widest part, but sparsely marked elsewhere. Length was 38.7 ± 1.5 mm (35.9 - 41.9 mm, n = 28) and width was 28.1 ± 0.6 mm (27.1 - 28.9 mm, n = 28). Mean fresh weight was estimated as 16.1 g (Chapter 1).

Eggs of Snares and Chatham Island Snipes differed in their size, colour and markings (Fig. 7.1), but both species laid eggs that weighed 19 - 20% of mean female body-weight (Chapter 1). Egg-weights of birds do not increase in direct proportion to body-weight; a regression equation for Charadriiformes was given by Rahn *et al.* (1975). Eggs of Snares Island Snipe (mean female body-weight 116.0 g) were 22.8% larger than expected, whereas those of Chatham Island Snipe (85.4 g) were only 3.9% larger than expected. Large eggs are considered an adaptation to a poor or unpredictable food supply, as the young hatch more fully developed and/or with a large yolk supply to compensate for the low rate of food intake after hatching (Martin 1987 and references therein). The relatively (and absolutely) larger eggs of Snares Island Snipe may indicate that food is less available on the Snares Islands during the breeding season than on Rangatira Island.

Incubation

Snares Island Snipe: Three 24-h watches at three nests with shared incubation revealed that males incubated for 60.4 - 64.0% of the time, and females 36.0 - 39.6% (Chapter 2). However, 531 spot checks at 32 nests throughout the day and night revealed almost equal sharing of incubation by the sexes (Fig. 7.3). Males tended to incubate from midnight to dawn (c.0600 hrs) and females from dawn to noon or early afternoon. There were frequent changeovers during mid-afternoon through to dusk, with either bird sitting at nightfall (c.2200 hrs).

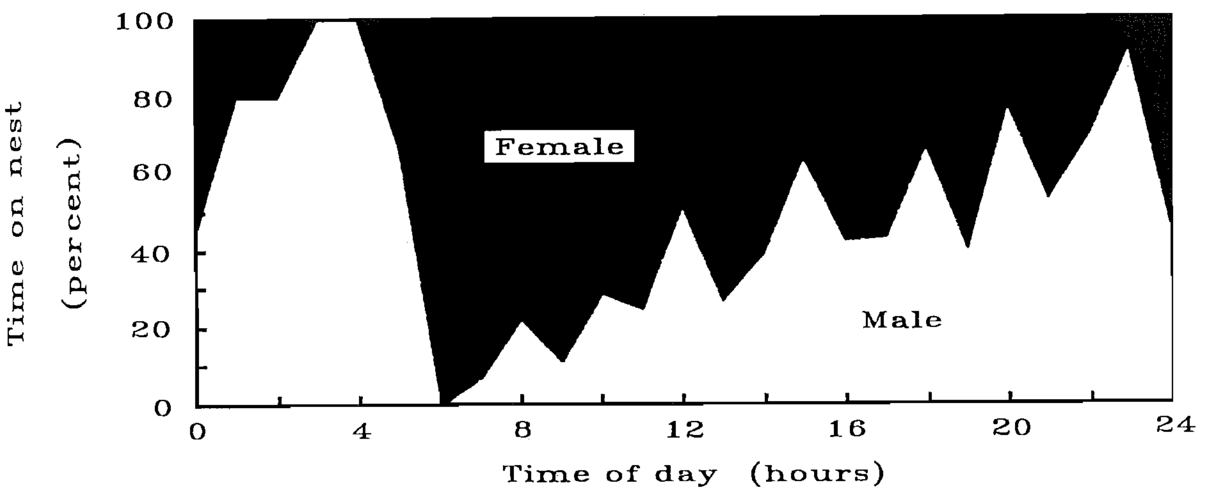

Figure 7.3. Daily pattern of incubation sharing by male and female Snares Island Snipe based on 531 spot checks at 32 nests. Males were on nests 51.3% of the time, and females 48.7%.

As male Snares Island Snipe did most of the nocturnal incubation, females were able to forage at night. At night, snipe frequently were seen up to 120 m from the nearest cover (Appendix 4), feeding in exposed swards of *Callitriche antarctica* and *Crassula moschata* that they did not use during the day. These swards contained huge numbers of amphipods (up to 12 000/m^2; pers. obs.), a major snipe food (Appendix 5). Nocturnal foraging by female snipe during incubation may have evolved to allow rapid recovery from the energetic stress of egg production; the clutch represents about 41% of female body-weight for Snares Island Snipe.

The longest incubation shift recorded for a male at three nests was 12 h 48 min. For females, the longest incubation shifts recorded were 8 h 32 min (nest with shared incubation; three nests observed) and 10 h 27 min (at one nest with female-only incubation; Chapter 2).

The well-concealed nests of Snares Island Snipe were very difficult to find. Recognising the incubation pattern (Fig. 7.3) greatly improved my nest-finding; the same technique may be useful for locating nests of Auckland Island and Antipodes Island Snipes. Male *Coenocorypha* snipes defended their territories with loud calls - a vibrant *chup* repeated 5 - 19 times at a rate of about twice per second, and/or a disyllabic *queeyoo* repeated 2 - 5 times (Warham 1967, Warham & Bell 1979, Appendices 1 & 4). Female snipe occasionally answered their mate's call with a softer *chur* repeated 2 - 4 times. Between 0600 hrs and 1200 hrs most male snipe were foraging (Fig. 7.3) but I could prompt them to call by playing back tape-recorded territorial calls. If a male called within 20 m of the nest, his incubating mate often replied and then I could usually find the nest after a few minutes' searching. Pairs that were not incubating typically foraged together; I would start nest-searching whenever I made regular sightings of a solitary bird from a known pair.
Chatham Island Snipe: 58 spot checks at 10 nests between 0600 hrs and 0200 hrs revealed no pattern in diurnal division of labour by the sexes. Between these hours, 67.2% of records were of females and 32.8% of records were of males. Observations were too few to show whether females spent more time on the nest than males; if males incubated more from 0200 to 0600 hrs, incubation could have been shared equally.

Hatching

Snares Island Snipe: The eggs hatched at any time of the day or night (determined to ± 5 h for 28 eggs). The two eggs of the clutch hatched 5 h 3 min ± 4 h 32 min apart (0 - 12 h 40 min, n = 11). The time spent in the nest was determined to within 1 hour for five chicks, and ranged from 2 h 48 min to 12 h 43 min (mean 6 h 41 min). Chicks that hatched out overnight were kept in the nest until dawn; likewise, chicks stayed in the nest longer during wet or cold conditions. Egg shells were left in the nest (n = 28) or within 0.5 m of it (n = 2).

The male led the first chick from the nest in all 10 double-chick broods observed during hatching. At four nests where only one egg hatched, the male took the chick in two cases and the female in two. In the first two cases the remaining egg was infertile or the second chick died while hatching. In the second two cases the second egg had been cracked and addled well before the eggs were due to hatch, and so when one egg has hatched, the female may not continue to sit on the second egg if it is noticeably damaged. Single eggs left in the nest were not incubated for more than a day after the first egg hatched.

Two of twelve pairs of New Zealand Snipe swapped their chicks within the pair within a day of leaving the nest, but no other within-pair exchange was recorded. One between-pair chick-swap was observed; a male swapped his 2 - 3 week old chick for the 3 - 4 week old chick of a neighbouring female. Each adult cared for the 'fostered' chick for at least 20 days after the swap was first noticed.

The sex of chicks was independent of the sex of the adults caring for them (n = 28, X^2 = 0.144, P = 0.71).

Brooding was observed only on the day of hatching. Chicks were fed entirely by adults for the first fortnight; the youngest chick seen to feed itself (probing) was 13 days old (culmen length 28.3 mm).

The sexes were equally good as parents with respect to growth rate and survival of the chicks. Increase in weight of chicks (g/day) reared by either sex was similar (Parallel curve analysis; $F_{1,84}$ = 1.015, n.s.). Chick survival until my departure from the Snares Islands (83% for 41 cared for by males; 77% for 34 cared for by females) and until age one-year-old (37% for male-parented; 32% for female-parented) did not differ between the sexes of parents (X^2 = 0.054 and 0.072, n.s., respectively).
<u>Chatham Island Snipe</u>: The eggs also hatched at any time of the day or night (n = 8). At four nests, the two eggs hatched 7 h 36 min ± 7 h 3 min apart (range 2 h 30 min - 18 h). Five chicks spent 1 h 15 min to 11 h 15 min in the nest (mean 7 h 09 min). At five nests where both eggs hatched, the male took the first chick to leave the nest.

Chatham Island Snipe were observed brooding young only on the day of hatching. The youngest chick seen probing was 18 days old (estimated culmen length 27.9 mm).

Development of young

At hatching

Snares Island Snipe: Newly-hatched chicks had uniformly dark grey down tipped with pale brown, slightly paler ventrally (Fig. 7.4a). A thin blackish line extended from the nostril to the eye, and another reached the top of the crown from the base of the culmen. The overall appearance was of uniform charcoal grey with flecks of brown. The bill was black, and the legs and feet grey with black on the sole and the back of the tarsus. The egg tooth was lost within a day of hatching (n = 7). Measurements of 28 chicks at hatching were: culmen-length 15.8 ± 0.7 mm (14.3 - 16.6 mm); tarsus-length 19.3 ± 0.7 mm (18.0 - 20.5 mm); mid toe & claw-length 26.8 ± 0.9 mm (25.0 - 28.5 mm). Weight was 15.5 ± 0.9 g (14.0 - 18.0 g).

a.

b.

Figure 7.4.a. Newly hatched Snares Island Snipe chick.
7.4.b. Newly hatched Chatham Island Snipe chick.

Chatham Island Snipe: The chicks (Fig. 7.4b) had dark grey down with brown and buff tips, more rufous on the nape, but the same head markings as Snares Island Snipe. The overall appearance was of pale rufous brown because of more brown on the tips of the down feathers. The bill was black, and the legs and feet lead grey, darker on the sole and the back of the tarsus.

Measurements of 12 chicks at hatching were: culmen-length 12.7 ± 0.6 mm (11.5 - 13.5 mm); tarsus-length 16.8 ± 0.6 mm (16.0 - 17.7 mm); mid toe & claw-length 22.4 ± 0.8 mm (20.9 - 23.4 mm). Weight was 11.0 ± 0.7 g (10.0 - 12.0 g).

Feather development

Feather development and down loss of Snares Island Snipe chicks took about 7.5 weeks (Table 7.1). Plumage development of Chatham Island Snipe chicks was similar to that outlined for Snares Island Snipe (based on 23 handlings of Chatham Island Snipe chicks 13 - 51 days old). However, after day 40, Chatham Island Snipe lost their down more rapidly and had shed the last traces by day 47 (n = 4). The youngest Chatham Island Snipe chick seen to fly was about 3 weeks old (Mike Dennison *in litt.*).

Table 7.1. Plumage development of Snares Island Snipe chicks, based on 160 handlings of known-age chicks between hatching and 78 days old. N = number of chicks handled per time interval.

Age (days)	N	Development
0 - 6	40	Totally downy
7 - 10	8	Scapular feathers starting to emerge from sheaths, belly feathers in sheath
11 - 13	7	Scapular feathers 10 mm out of sheaths, primaries in sheath
14 - 16	7	Back and part of belly and flanks well feathered; primaries 1 - 9 mm out of sheaths
17 - 19	10	Extensive down, thinning on back and belly; primaries 6 - 14 mm out of sheaths
20 - 23	12	Well feathered; dense down around head and rump, sparse elsewhere; primaries 12 - 32 mm out of sheaths
24 - 27	12	Down on head and rump, sparse on upperwing coverts, traces elsewhere; primaries 27 - 53 mm out of sheaths
28 - 35	21	Fully feathered; down on head and rump, traces on upperwing coverts; primaries 40+ mm out of sheaths; can flutter along ground from day 30
36 - 44	17	Down on nape, chin and frons, trace on rump
45 - 53	14	Trace of down on nape
54+	12	Down-free

Growth rates

The asymptotes for six growth parameters of Snares Island Snipe chicks fell between the mean adult male and mean adult female measurement for each parameter (Table 7.2), indicating that chicks reached full adult size in all parameters soon after independence. The asymptote for

Chatham Island Snipe chick weight was only 96% of mean adult male weight, but the other three asymptotes (Table 7.2) all exceeded mean adult male dimensions. Snares Island Snipe chicks had exceeded 95% of the asymptote for all parameters by the time they reached independence (age c.65 days; Chapter 1). Chatham Island Snipe chicks did not attain 95% of the asymptote for weight and culmen until about a week after becoming independent (age c.41 days; Chapter 1).

Table 7.2. Characteristics of the Gompertz growth equations determined for Snares Island Snipe and Chatham Island Snipe chicks. (See Methods for details.) Growth equations for Snares Island Snipe could be used to estimate ages of chicks of the similar sized Auckland Island and Antipodes Island Snipes. Asymp. = asymptote*.

Parameter	Start time (days)	Gompertz constants *A*	*C*	*D*	*M*	r^2	Asymp.	Time to 95% Asymp. (days)
S.I. Snipe								
Weight	1	-45.88	150.54	0.06	-1.17	0.95	104.66	59.6
Culmen	0	-4.18	62.66	0.05	2.73	0.99	58.48	61.2
Tarsus	0	18.80	6.11	0.14	6.48	0.93	24.91	17.0
Mid toe & claw	0	6.27	27.61	0.08	-15.44	0.88	33.88	19.9
Wing	21	56.05	53.34	0.16	23.10	0.94	109.40	37.3
Tail	28	20.30	20.29	0.17	35.06	0.90	40.60	48.3
C.I. Snipe								
Weight	1	1.72	70.01	0.08	9.90	0.94	71.73	48.7
Culmen	0	10.13	35.13	0.07	12.72	0.99	45.26	49.8
Tarsus	0	15.95	7.50	0.10	7.53	0.95	23.45	25.4
Mid toe & claw	0	-709.59	740.81	0.05	-83.62	0.96	31.22	32.6

*Asymptote measurements in mm, except weight (g).

Chicks of Chatham Island Snipe were about 30% smaller than those of Snares Island Snipe (Fig. 7.5; Table 7.2). The growth constant (K_G) for Snares Island Snipe weight was 0.070, compared with 0.074 for Chatham Island Snipe, indicating similar growth rates for the two species (see also Fig. 1.3).

The culmen of Snares Island Snipe chicks grew much more slowly in relation to their growth asymptote than those of Chatham Island Snipe chicks (Fig. 7.6; Table 7.2). The growth constant for Snares Island

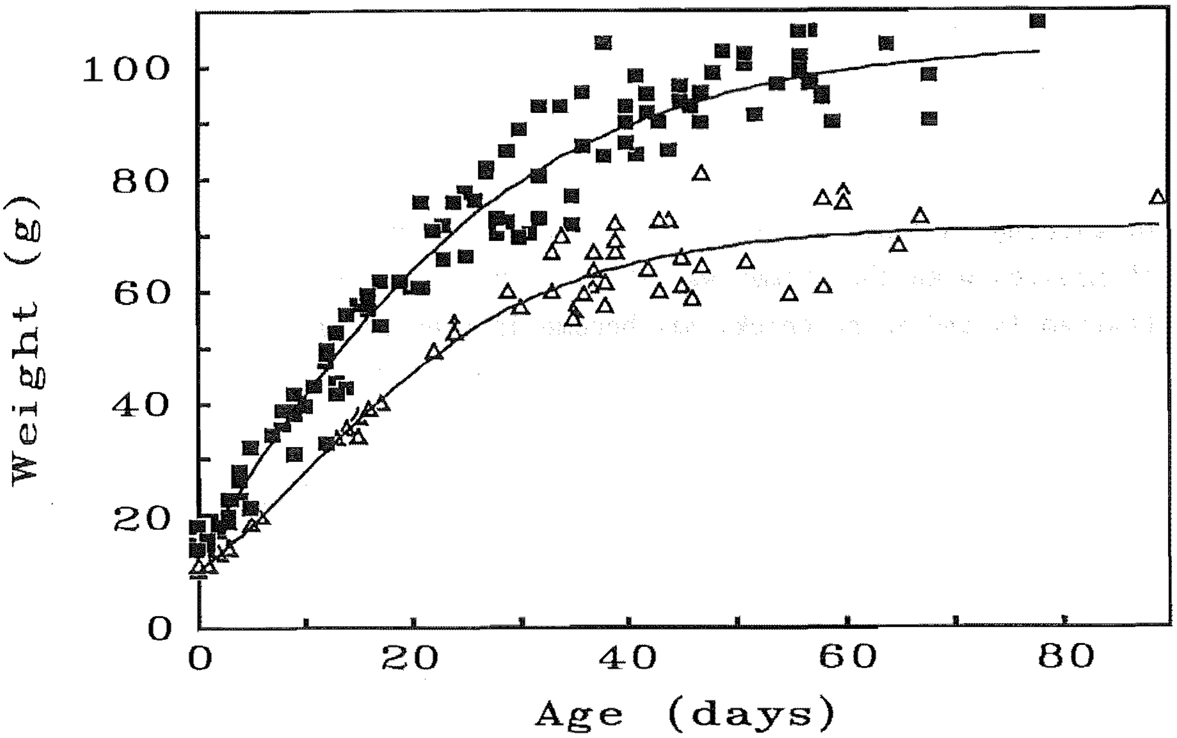

Figure 7.5. Weight gain of Snares Island Snipe chicks (solid squares) and Chatham Island Snipe chicks (open triangles). Details of Gompertz growth equations given in Methods and Table 7.2.

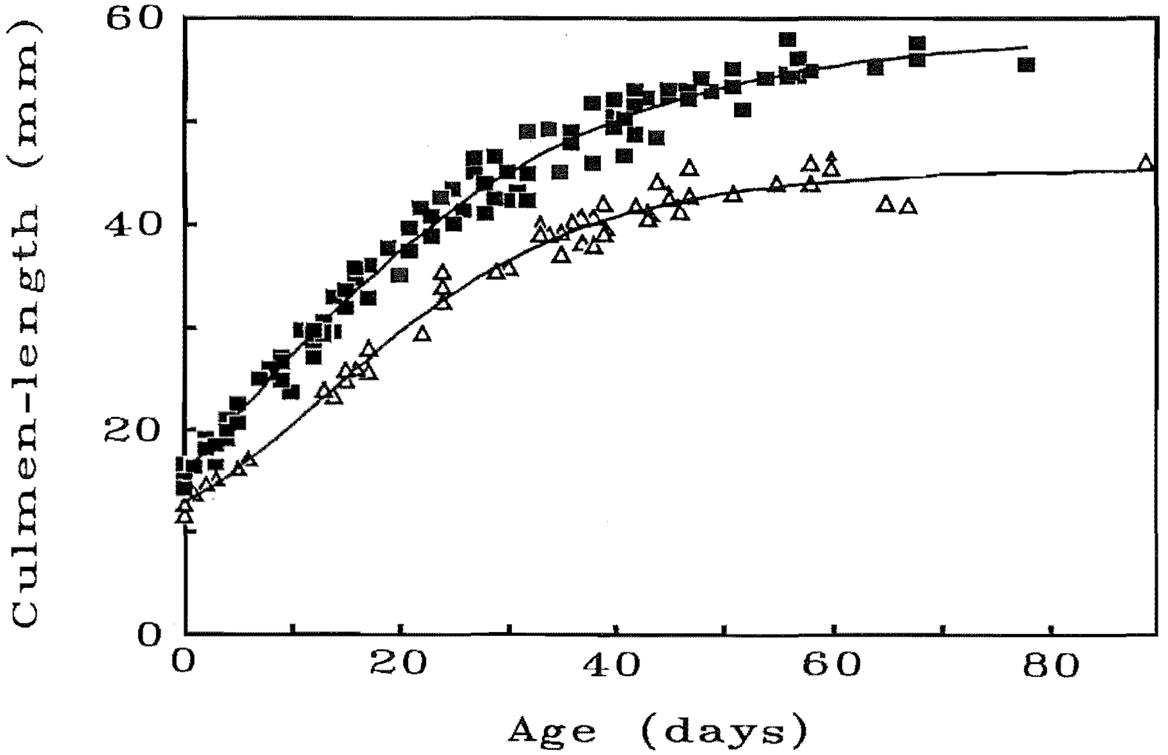

Figure 7.6. Culmen growth of Snares Island Snipe chicks (solid squares) and Chatham Island Snipe chicks (open triangles). Details of Gompertz growth equations given in Methods and Table 7.2.

Snipe culmen was only 0.055, 38.3% of that for Chatham Island Snipe (K_G = 0.143).

As snipe get all their food by probing in the soil (pers. obs.), bill-length must be a major constraint on the foraging ability of developing chicks. Chicks of both species started to probe for themselves when the culmen was about 28 mm long. With rapid bill growth, Chatham Island Snipe chicks may become independent sooner than Snares Island Snipe chicks (41 v. 65 days). However, Snares Island Snipe became independent 18 days later in relation to bill-length than Chatham Island Snipe, and so there may be behavioural as well as morphological differences between the two species in the development of foraging ability. Food may have been less available on the Snares Islands, prolonging the period of dependence on parental feeding.

Conclusion

Snares Island Snipe and Chatham Island Snipe were similar in their breeding ecology, although data on laying and incubation by Chatham Island Snipe are incomplete. Both species had prolonged breeding seasons during the spring and summer. Most matings were monogamous, with courtship feeding of the female by the male during egg-formation (Chapter 1) and shared incubation of the two-egg clutch. Nests were concealed under vegetation; solid overhead cover was a feature of Snares Island Snipe nests, probably as protection from crash-landing Sooty Shearwaters. Broods were split soon after hatching, the male caring for the first chick to leave the nest.

Chatham Island Snipe differed from Snares Island Snipe in breeding two months earlier and laying smaller eggs. The bill of Chatham Island Snipe chicks grew more rapidly and they attained independence three weeks sooner than Snares Island Snipe chicks. These differences in breeding ecology may have been due to differences between the two islands in the timing and size of annual peaks in prey abundance. This hypothesis could be tested by systematic sampling of soil invertebrates during spring and summer on Rangatira Island by techniques similar to those used on the Snares Islands (Chapter 5).

Appendix 3

The Little Barrier Island snipe.

Notornis 35 (1988): 273-281.

Reprinted from NOTORNIS, Vol. 35, Part 4. December 1988: p.p. 273-281

THE LITTLE BARRIER ISLAND SNIPE

By C. M. MISKELLY

Booklet to accompany thesis by Colin M Miskelly "Social and Behavioural constraints on Breeding by New Zealand Snipe"

THE LITTLE BARRIER ISLAND SNIPE

By C. M. MISKELLY

ABSTRACT

A single snipe was captured on Little Barrier Island in 1870. The history of this specimen is traced up to its designation as the holotype of *Coenocorypha aucklandica barrierensis* 85 years later. Other records of snipe in the Auckland area seem to refer to the one Little Barrier specimen or to other species of wader.

Snipe apparently disappeared from Little Barrier Island in the 1870s, when cats became established, but apparently were rare before then. References by R.H. Shakespear to "snipe" on Little Barrier Island are given, but are regarded as probably referring to other species.

THE SPECIMEN FROM LITTLE BARRIER ISLAND

On 10 October 1870, Captain F.W. Hutton exhibited a specimen of snipe to a meeting of the Auckland Institute (Hutton 1871a). The bird had been "captured at the Little Barrier Island by Captain Bennett, of the schooner *Mary Ann*, and presented to the institute by Mr. T.B. Hill". Hutton stated that:

> Two specimens only were seen, of which the one now exhibited was caught alive but died in confinement: the other escaped. It answered tolerably well to the description of *Gallinago pusilla*, Buller, although it appeared rather larger than that bird and somewhat different in colour. But as Buller's description was from the single specimen captured at the Chatham Islands, much importance could not be attached to the discrepancies, which were of a trivial nature.
>
> Mr. Baber stated that he had seen this bird in Hobson's Bay, Auckland some years ago.

Buller (1869) had described his " Little Snipe" from the Chatham Islands only the year before, and no skins of Chatham Island Snipe were available to compare with the new specimen. The snipe was added to the collection of the Auckland Institute and Museum, then curated by T. Kirk (Curator, 1868-1874 – Powell 1967).

The next mention of the snipe in the records of the museum was in a large catalogue entitled *New Zealand and Foreign Vertebrates*. This register (the "Blue Book" of Gill 1984) was evidently made in 1898. The entry is in T.F. Cheeseman's handwriting, and reads:

Number	When Received	Name	From whom received	Locality
869	~~In Mus 1874~~	Gallinago pusilla	~~no history~~	Little Barrier Island
872	1870	Gallinago pusilla	Presented by Mr T.B. Hill	Raglan District

Cheeseman was Curator, Auckland Institute and Museum, from 1874 to 1923. The crossings-out were by Cheeseman (G. Archey, unpublished letter to E.G. Turbott, 9 March 1959). Archey interpreted the crossings-out as showing that Cheeseman "evidently thought *subsequently* that [869] was the Little Barrier specimen" (Archey's emphasis).

All subsequent records of snipe from the Auckland region were apparently based on the 1870 specimen, although there was some confusion in the literature. Cheeseman (letter to Buller, 2 June 1884) wrote "I have a specimen of *Gallinago pusilla* in the Auckland Museum, obtained by Mr. T.B. Hill in the Raglan district many years ago; but I have never met with the bird myself" (Buller 1888: 34). This was almost certainly the bird mentioned by Hutton (1871a) because the donor and the date (in the catalogue) are the same. The locality "Raglan District" was apparently attributed to the specimen in error (see below).

Buller (1888: 33) recorded *Gallinago pusilla* from the Chatham Islands, and "...the next record of its occurrence was from the Gulf of Hauraki, near Auckland" – then he went on to quote Cheeseman on the Raglan specimen. Buller's reference to a bird from the Hauraki Gulf must, therefore, have been based on either Hutton's (1871a) original report or Hutton (1871b), where the range of *Gallinago pusilla* was given as "Little Barrier Island and Chatham Islands".

Canon H.B. Tristram (1893), writing from England, further confused the issue with his apparent lack of local geographical knowledge. Tristram, referring to *Gallinago pusilla,* wrote: "Very few specimens have been received, but the species has twice been obtained in New Zealand (to which it is evidently an occasional wanderer): once by Sir James Hector in the Gulf of Hauraki, and once by Mr. F. [*sic*] B. Hill on Little Barrier Island." In 1893, the only published reference linking Mr Hill with a snipe from Little Barrier Island was Hutton (1871a), which Tristram must have seen. The reference to Sir James Hector is confusing, but I suspect that the answer can be found in the first paragraph on Chatham Islands Snipe in Buller (1888): "In 1868 I received from Dr. (now Sir James) Hector a small Snipe obtained by Mr. Charles Traill during a visit to the Chatham Islands". The mention of "the Gulf of Hauraki" comes later in the same paragraph. It is apparent that Tristram was unaware that "Little Barrier Island" and "the Gulf of Hauraki" could be referring to the same place; I further suggest that Tristram confused the bird obtained from the Chatham Islands via Hector with the locality "the Gulf of Hauraki".

The comment by Mr Baber (Hutton 1871a) that he had seen "*Gallinago pusilla*" in Hobson's Bay was repeated by Oliver (1955: 275) when describing the Little Barrier Snipe *Coenocorypha aucklandica barrierensis:*

> Snipe, possibly belonging to this subspecies, were reported as having been seen by Mr. J. Baker [*sic*] earlier in the century on the shore of Hobson Bay, Waitemata Harbour.

I agree with Turbott (1961) that Baber was probably referring to Arctic migrant waders.

The Little Barrier snipe specimen received little attention for 60 years after Tristram's (1893) comments. During this time the bird specimens in the Auckland Institute and Museum were renumbered, and a new catalogue, *New Zealand Mammals and Birds,* was filled in by L.T. Griffin, apparently between 1919 and 1922 (Gill 1984). Griffin was museum assistant and preparator of specimens from 1908 to 1922 and assistant curator from 1923 to 1935 (Powell 1967). The entries in this catalogue read:

Number	When Received	Name	From whom received	Locality	Remarks
185		Gallinago pusilla no sex		Little Barrier Island	AV 78.1
186	1870	Gallinago pusilla	Presented by:-T.B. Hill	~~Raglan District~~	AV 78.2, 1389.1 See Proc. NZ Inst. vol.3, p. 86.

The crossing-out, arrow, and comments in the remarks column were made by E.G. Turbott in 1953 (unpublished letter to Archey, 15 April 1959). Turbott was Ornithologist at Auckland Institute and Museum from 1946 to 1957 (Powell 1967).

Griffin started to transcribe all the details from *New Zealand Mammals and Birds* to cards in 1924, and gave each specimen an "AV" number (B.J. Gill *in litt.*).

In 1953, W.R.B. Oliver (unpublished letter to Turbott, 24 April) asked about the snipe from "the Raglan District" mentioned by Buller (1888) and asked to borrow the specimen from the Auckland Institute and Museum. On receiving the specimen, Oliver realised that it was distinct from the other forms of New Zealand snipe, and that it may have been the one mentioned by Hutton (1871a) from Little Barrier Island. Oliver's comments prompted Turbott (unpublished letter to Oliver, 3 August 1953) to search through the old consecutive catalogue and discover the mix-up in labelling of "185" and "186". Turbott and Oliver agreed that 186 was the bird mentioned by Hutton (1871a), and Turbott suggested that the locality "Raglan" had been given in error by either Cheesman or, more likely, Kirk, who was Curator in 1870.

If 186 was the Little Barrier Island specimen, why was 185 labelled "Little Barrier Island"? Turbott (unpublished letter to Oliver, 3 August 1953) suggested that "185 was a stray bird in the collections and that the locality 'Little Barrier Island' had been attached to it by mistake", and posted both specimens to Oliver.

Oliver (unpublished letter to Turbott, 9 August 1953) recognised 185 as an Auckland Island Snipe *C. a. aucklandica:*

> The large one is aucklandica so doesn't alter the position as regards the small one. It does in a way confirm the locality of the small specimen as Little Barrier Island, as obviously this locality is wrong for the large bird but presumably was intended for the small bird, Cheeseman evidently forgetting which one came from Little Barrier Island. Raglan is I suppose Hill's address. Taking all things together I think it is safe to say that the small specimen which does not definitely agree with any described subspecies, comes from Little Barrier Island, was collected by Captain Bennet [*sic*], and given to the Museum by T.B. Hill.

It was at this stage that Turbott made the changes to Griffin's entry in the catalogue (Turbott, unpublished letter to Archey, 15 April 1959).

Oliver (1955: 275) described the Little Barrier Snipe as a new subspecies, *C. a. barrierensis*, based on the unique specimen in the Auckland Institute and Museum. The specimen (now AV 1389. 1, Fig. 1) is most like the Stewart Island Snipe *C. a. iredalei* in size (Table 1). The bird, which had

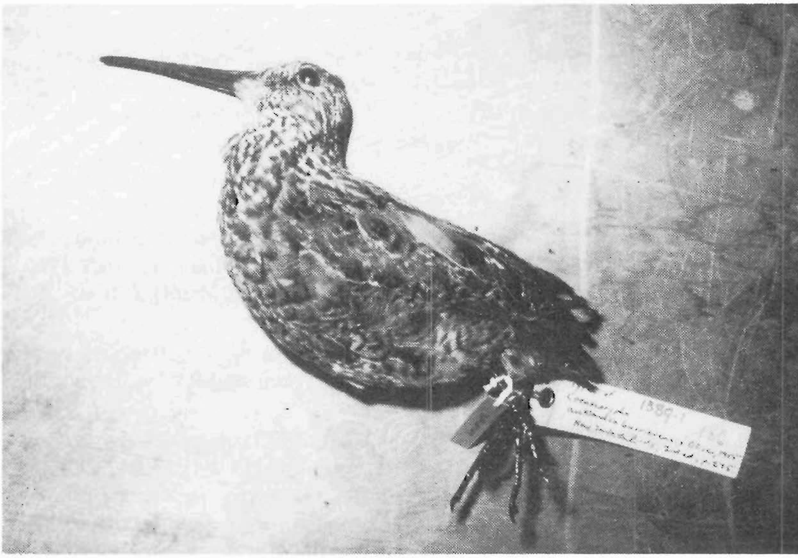

FIGURE 1 — The Little Barrier Island snipe, Auckland Museum AV 1389.1

been mounted as a display specimen, is very faded on its right side; the left side may also be somewhat faded. Compared with *C. a. iredalei*, the Little Barrier snipe has a greater amount of buffy white on the chin and throat, has light, mid-brown crescentic subterminal bars from upper throat to mid-belly, and has the lower belly unbarred. Stewart Island Snipe have a heavy gorget of blackish blotches extending from upper throat to lower breast, and their belly is buffy white with some blackish bars. Overall, *C. a. barrierensis* has finer, lighter markings on the undersurface, compared with the bold gorget of *C. a. iredalei*.

TABLE 1 — Comparison of measurements of the holotype of *Coenocorypha aucklandica barrierensis* (LBI) with measurements from skins of *C. a. iredalei* in Canterbury Museum, National Museum, and British Museum (Natural History). All measurements in millimetres.

	LBI	*C. a. iredalei*			
		$\bar{x}$	n	SD	Range
Culmen	51.9	53.1	11	3.40	46.1 - 58.3
Tarsus	21.3	24.0	7	0.64	23.2 - 25.0
Mid-toe and claw	29.0	33.0	5	1.11	32.2 - 34.9
Tail	32.0	39.8	6	1.83	36.7 - 41.6
Wing	103	108	7	2.8	105 - 113

There was further correspondence on the Little Barrier snipe between Turbott (then Assistant Director and Keeper of Zoology, Canterbury Museum) and Sir Gilbert Archey (Director, Auckland Institute and Museum, 1924-1964) from February to April 1959. Turbott was working on a manuscript on the birds of Little Barrier Island (published in Hamilton 1961) in which he included an account of the snipe. This correspondence culminated in Turbott writing a new label for the Little Barrier specimen and Archey assigning it a new catalogue number as the holotype for *C. a. barrierensis* (Gill 1983). After 89 years in the collections of Auckland Institute and Museum, the Little Barrier snipe had been recognised as distinct and the true collection details were entered on its label.

Oliver was quite correct when he guessed that Raglan was Hill's address. Turbott succeeded in tracing T.B. Hill through the Waikato Branch of the Royal Society and the Raglan Old Settlers' Association; the following information is from unpublished letters to Turbott from C.G. Hunt in February and March 1962.

Thomas Boucher Hill owned a chemist's shop in Mt Eden (Auckland) and bought a farm in the Te Mata district near Raglan in the late 1860s. He eventually sold his Mt Eden business and set up as a chemist in Raglan township, where, in the absence of a local medical practitioner, he was in effect the local doctor. Mr Hill had many interests, not least of which was a keen interest in natural history. He died in Raglan about 1920, aged 88, and is buried in the Raglan graveyard.

One mystery remains: what was the provenance of 869 (now AV 77.4), an Auckland Island Snipe with no collection data, that once bore the locality "Little Barrier Island"?

SNIPE ON LITTLE BARRIER ISLAND

Although the unique specimen of *C. a. barrierensis* has received sporadic attention over the years, little is known about the fate of snipe on Little Barrier Island. Turbott (1961) suggested that snipe became extinct owing to the introduction of cats.

When cats were introduced to Little Barrier I. is uncertain. They were certainly present by 1885, along with wild pigs and dogs (Reischek 1886b, 1886c, 1886d, although Hamilton 1961: 134 suggested that pigs on Little Barrier Island were confined to a small area of coastal forest behind Ngamanauraru Bay). Reischek visited Little Barrier Island five times between October 1880 and May 1885 (Reischek 1887a). Referring to the Stitchbird (*Notiomystis cincta*), Reischek (1886a) wrote:

> These very rare birds will soon disappear, even from these lonely wilds, owing to the domestic wild cats, which are very numerous, and commit great havoc among them. . . .

There is circumstantial evidence that cats became established on Little Barrier I. in the 1870s: Hutton (1869) reported Saddlebacks (*Philesturnus carunculatus*) as very common on a 4-day visit in December 1867, whereas Reischek (1887b) found them to be rare in October 1880, still scarcer in October 1882, and not at all subsequently. Turbott (1947 and 1961) argued that cats were responsible for the extinction of Saddleback on Little Barrier I.; this is supported by the successful reintroduction of Saddleback to the island in 1984, after the eradication of cats by the NZ Wildlife Service in 1980 (Veitch 1985).

Veitch (1985) gave the date of cat introduction as "about 1870", on the strength of Hutton's (1869) and Reischek's (1887b) observations (C.R. Veitch, pers. comm.).

If cats did become feral on Little Barrier I. in the 1870s, this agrees well with the presumed date of disappearance of snipe, the only record of snipe on Little Barrier Island being the two seen in 1870 (Hutton 1871a). However, snipe were probably rare on Little Barrier Island even before cats were present, as Layard (1863) and Hutton (1869) did not record snipe. Reischek (an avid collector of rare birds) made no mention of seeing snipe during his "ten months" on the island between 1880 and 1885.

I suggest that snipe were scarce on Little Barrier I. in 1870 because of predation by kiore (*Rattus exulans*), and perhaps wild pigs and dogs. No other form of New Zealand snipe is known to have survived in the presence of any species of rat (Miskelly 1987). Perhaps kiore had not, in 1870, been on Little Barrier I. long enough to eliminate snipe. The introduction of cats would have sealed the fate of snipe.

However, there are records of "snipe" from Little Barrier I. long after cats were introduced.

Little Barrier I. was purchased as a reserve for the preservation of rare birds in 1894 (Hamilton 1961). The last of the previous Maori owners were removed in 1896. R.H. Shakespear, appointed curator of Little Barrier Island Reserve by the Auckland Institute, was on the island from 19 January 1897 until 28 February 1910 (Hamilton 1961). During his 13 years on Little Barrier I., Shakespear kept a meticulous diary, which included many natural history observations, and he also corresponded frequently with T.F. Cheeseman (then Curator of Auckland Institute and Museum and Shakespear's superior). These unpublished diaries and letters are in the Auckland Institute and Museum Library; I thank Ian Thwaites for permission to quote from them.

Shakespear made several references to "snipe" or snipe-like birds; these are quoted as written:

Wednesday 29 September 1897 (diary)

> Gloriously fine day...went around in the boat to the west side in order to collect the remains of the whale...we also saw a beautiful little snipe. he was very tame & allowed us to approach within a few feet. he was feeding on the whale. the top of his head was a rich brown. I saw no white stripe.

Monday 4 October 1897 (letter)

> ...They had very rough weather down here & never expected to see me. there had been an unusually severe Easterly gale with high tides & there was a heavy sea running here on Monday [27 September]...I am sorry to say the whale was washed away, but so far we have managed to collect most of the bones...I noticed a most beautiful little snipe feeding on the remains. he was a real snipe. & very tame. his markings were rather more like a woodcock than a snipe. yesterday when we put him up he flew up Turner's Gully, so perhaps he may remain here.

There used to be a snipe many years ago indigenous to the island but this one seems to me more like the Auckland Id. species. however he is a very welcome visitor & his flight made me think of other days. he had a reddish brown patch on his head - & his markings were much darker than the ordinary snipe more mottled on the wing feathers.

Wednesday 27 October 1897 (diary)

Fine day. S.S.W. breeze...Saw a large snipe today, a different variety to the one we saw by the whale. this bird seemed rather larger than the English snipe.

Friday 29 October 1897 (letter)

I told you that we saw a beautiful little snipe by the whale's remains. it stayed about for some time. the patch on the top of its head was a rich dark brown. yesterday I saw another snipe he was down by the boathouse. he was a far larger bird, & breast & wing feathers lighter. he got up just like an ordinary snipe & gave the same cry. the boy saw him feeding up Turner's this morning close to the creek. I think he is altogether another variety."

Monday 1 November 1897 (diary)

It commenced to rain this morning about 5 a.m. & continued until 9 a.m...I saw the bird that I thought was a snipe. It is far larger than the real snipe which we saw at the carcase of the whale.

This is a very handsome bird & very tame. I am going to try & get a photo. about 8 inches long. strong pointed beak. about 1½ inches long. palish brown with greyish white tint which ran through all the feathers, so that looking at him you would say he was greyish white deepening into a rich brown on the back. Sides of the throat whitish grey. brown patch on the top of the head, but not nearly of such rich a hue as the little snipe.

Thursday 6 October 1898 (diary)

Squally morning. Wind S.W. fresh breeze.

The children saw a bird which they describe as something like a snipe with a very long beak. it was on the spit. probably I shall come across it tomorrow.

Friday 7 October 1898 (diary)

Cloudy morning. Westerly wind. fresh breeze.

In the evening we caught a bird something like a large curlew. it was nearly dead with exhaustion & want of food. it tried to swallow the worms we gave it, but could not & died during the evening so I shall put it in spirits for Mr. Cheeseman.

Monday 20 November 1899 (diary)

Weather. raining hard. Wind Northerly.

I was along at the spit in the morning & again at sunset. I flushed the Little Barrier Snipe, & he went up Turner's Crk. (he has been about now for about 10 days).

Sunday 14 September 1902 (diary)

Weather - stormy, sky windy, scud coming over fast from W.S.W. Wind W. strong breeze, glass inclined to rise. some sea on the west landing. A specimen of the "Little Barrier Snipe" was on the lawn this morning he was very tame, & I had a good look at it through the glasses. it was very tame & in the evening was still on the lawn at the back of the house.

Sunday 19 October 1902 (diary)

Weather. squally. sky cloudy. thick over the mainland. Wind, Sou West: strong breeze. fair sea on. glass low & steady...Blowing & raining all day. heavy sea running...A whip of snipe about 15 were on the flat yesterday, & today. I have not seen any like them before. They are very handsome little birds. I watched them for some time through my field glasses.

Wednesday 2 November 1904 (diary)

> Weather, improving, sky, cloudy with sunshine. Wind, Sou West moderate breeze...The "snipe" still remain round the house.

It is apparent than Shakespear used "snipe" as a general term for shorebirds. I suggest that most, if not all, of the sightings refer to stray Arctic or local waders. First, all the records are from September to November, when Arctic waders are arriving in New Zealand from their breeding grounds. Secondly, all but one of the records followed bad weather and strong winds – likely conditions for migrants to get blown off course. Thirdly, all of the sightings were from the coast or around Shakespear's house at Te Maraeroa – likely habitats for vagrant waders.

From my own experience with New Zealand snipe and Little Barrier Island, I suspect that snipe would have survived longest in areas of sedge at the mouths of streams and wherever damp, forested gullies had dense ground cover. New Zealand snipe are not known to feed in the open during the day and so would be unlikely on a lawn. Shakespear also mentioned flushing snipe and having them fly considerable distances. It is unusual for extant forms of New Zeland snipe to fly more than 30 m if flushed during the day (pers. obs.), although *C. a. barrierensis* was apparently the form of *Coenocorypha* that flew best (Miskelly in prep.).

If Shakespear was not seeing Little Barrier Snipe, what was he looking at? Six species of waders have been recorded as stragglers to Little Barrier I. Hutton (1869) and Reischek (1887a) recorded Variable Oystercatcher (*Haematopus unicolor*), Turbott (1961) recorded Banded Dotterel (*Charadrius bicinctus*), Far-eastern Curlew (*Numenius madagascariensis*), Bar-tailed Godwit (*Limosa lapponica*) and Pied Stilt (*Himantopus himantopus*), and Veitch (pers. comm.) reported Least Golden Plover (*Pluvialis fulva*); other species are likely also.

The bird seen on 29 Sep 1897 may have been a Sharp-tailed Sandpiper (*Calidris acuminata*), judging by its small size, the reddish-brown top of its head and "no white stripe". The larger, greyish "snipe" with a 1½ inch bill of 27 Oct - 1 Nov 1897 may have been a Knot (*Calidris canutus*) or New Zealand Dotterel (*Charadrius obscurus*). The "large curlew" caught on 7 Oct 1898 cannot be traced in the collections of Auckland Institute and Museum (B.J. Gill, pers. comm.).

Shakespear's other records are too vague to allow speculation as to identity, but the 15 birds seen on 19 Oct 1902 were obviously not snipe, which do not flock. The balance of evidence suggests that snipe disappeared from Little Barrier I. soon after they were discovered in 1870.

ACKNOWLEDGEMENTS

I am indebted to Dr Brian Gill (Curator of Birds, Auckland Institute and Museum) for allowing access to the Little Barrier snipe specimen, providing copies of the Oliver/Turbott, Turbott/Archey and Turbott/Hunt correspondence, and answering many queries about the early days of the Institute. I am very grateful to Ian Thwaites and Peggy Sayes (Auckland Institute and Museum Library) for locating the snipe references in Shakespear's diaries and letters and giving permission to quote from them.

The manuscript was improved by comments from Brian Gill, Barrie Heather, Ian McLean, Graham Turbott and Richard Veitch. Funding was provided by the Department of Conservation (formerly Department of Lands & Survey) and the Royal Forest & Bird Protection Society.

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Appendix 4

Aerial displaying and flying ability of Chatham Island Snipe and New Zealand Snipe.

Emu (in press).

Abstract

Chatham Island Snipe *Coenocorypha pusilla* and New Zealand Snipe *C. aucklandica* were studied intensively during one and six breeding seasons respectively, and observations of aerial displays and related behaviours recorded. Chatham Island Snipe gave three types of acoustic aerial displays. The displays were performed only at night. Type 1 was a strident monosyllabic call, also given in several contexts on the ground. Type 2 was a series of disyllabic calls identical to a common territorial display given on the ground. Type 3 began with a series of disyllabic calls and ended with a non-vocal 'roar' considered homologous to the 'drumming' displays of *Gallinago* snipes. Evidence for non-vocal acoustic displaying by three subspecies of New Zealand Snipe is discussed. The intensively studied Snares Island Snipe *C. aucklandica huegeli* was not seen to give aerial displays. Chatham Island Snipe were flushed significantly more frequently and flew further than Snares Island Snipe, and had significantly lower wing-loadings. The aerial displays of Chatham Island Snipe were similar to descriptions of aerial displays of the 'Chubbia' snipes of South America: Cordilleran Snipe *Gallinago stricklandii*, Andean Snipe *G. jamesoni* and Imperial Snipe *G. imperialis*.

Introduction

Snipe (Scolopacidae: Gallinagonini) are well known for their complex aerial displays. Of the 15 species in the genus *Gallinago*, only the lek-breeding Great Snipe *G. media* does not have an aerial display. The other 14 species all have a non-vocal acoustic component in their aerial display ('drumming' or 'bleating'), generally accepted to be caused by air currents vibrating the rectrices as the birds dive at speed (Tuck 1972, Sutton 1981, Hayman *et al.* 1986). The monotypic Jack Snipe *Lymnocryptes minimus* also has an acoustic aerial display; this is considered to be mainly vocal (Sutton 1981), although Blair (1936) described a whirring noise rather like the drumming of Common Snipe

G. gallinago, thought to be produced by the 'pinions'.

The remaining genus of snipe comprises two species now confined to four isolated island groups off New Zealand: New Zealand Snipe *Coenocorypha aucklandica* which occur on the Snares (*C. a. huegeli*), Antipodes (*C. a. meinertzhagenae*) and Auckland (*C. a. aucklandica*) Islands, and Chatham Island Snipe *C. pusilla*. *Coenocorypha* snipes have often been described as lacking aerial displays (Manson-Bahr 1931, Warham 1970, Tuck 1972, Johnsgard 1981, Jehl & Murray 1986). However, Miskelly (Appendix 1) presented evidence for acoustic aerial displaying by *Coenocorypha* snipes, and argued that the nocturnal aerial display of the extinct Stewart Island Snipe *C. aucklandica iredalei* was the legendary hakawai, a mystery bird of the Maori people in New Zealand.

Here I present sonagrams of three types of aerial displays by Chatham Island Snipe and discuss evidence for aerial displaying by three subspecies of New Zealand Snipe. To investigate the flying ability of Chatham Island Snipe and Snares Island Snipe I compared wing-loadings, assuming that forms with smaller wings in relation to body size (i.e. higher wing-loadings) had reduced flying ability. These results are compared with assessments of the flying ability of these two forms obtained in the field. Aerial displays of *Coenocorypha* snipes are compared with published accounts of displays by other snipes.

Study areas and methods

Chatham Island Snipe were studied among *Olearia traversi*/*Plagianthus regius* forest on Rangatira (South East) Island Nature Reserve (44°21'S 176°10'W), Chatham Islands, 25 November 1983 to 18 January 1984, and 7 - 15 July 1986 (61 days, 20 nights). Snares Island Snipe were studied under *Olearia lyalli* forest on Main Island, Snares Islands Nature Reserve (48°01'S 166°36'E) during 477 days and 134 nights of fieldwork between December 1982 and December 1987; research was carried out in the months September to March inclusive, and encompassed six breeding seasons. Snipe were sexed by measurements (females are larger; unpubl. data) and by sex-specific calls after colour-banding.

Tape recordings of nocturnal aerial displays by Chatham Island Snipe were made with a Sanyo M 1150 cassette recorder and a BST super-cardioid condenser microphone on 9 January 1984 and 11 July 1986. The acoustic components of the displays were analysed on a Kay Sonagraph 6061-B, using the 80-8000 Hz scale (linear setting) and the wide band pass filter.

Flushing rates of snipe (proportion of nights when snipe were flushed) were recorded. Distances that snipe flew after flushing were estimated to the nearest 5 m (up to 20 m) or nearest 10 m (up to 70 m).

Left wing outlines (primaries slightly spread) of 29 live adult Chatham Island Snipe (15 ♂♂, 14 ♀♀) and 29 live adult Snares Island Snipe (16 ♂♂, 13 ♀♀) were traced on to paper. Wing areas were determined from outlines using a polar planimeter (mean of three replicates from each of two pole positions). Moulting birds were not included in the samples. Wing-loadings (Nm^{-2}) were calculated by multiplying the body mass (kg) of each bird by the acceleration due to gravity (9.8 ms^{-2}) then dividing by twice its measured wing area plus the dorsal area between the wings (m^2) (see Pennycuick 1987). All measurements are given as mean ± standard deviation. Comparisons of mean wing-loadings between sexes and populations were made using a jackknife test (Sokal & Rohlf 1981).

Results

Aerial displaying

Aerial displays of Chatham Island Snipe were heard on five (36%) nights in 1983-84, and two (33%) nights in July 1986. All seven nights on which displays were heard were calm and clear, but displays were not always heard on such nights.

Three types of aerial displays were recorded for Chatham Island Snipe (Fig. 9.1). Type 1 display was a strident *chep* or *yip* given continuously at the rate of one call every 0.8 s (n = 1), or as irregularly spaced single calls. The calls shown in Fig. 9.1a were given by a bird in fast horizontal flight about 20 m above the ground (observed in torch beam) on 11 July 1986. Type 1 calls were also heard from flying birds on 2 December 1983 and 8 July 1986. The same call was frequently given from the ground at any time of day or night and appeared to be contagious, with up to six birds of both sexes calling on the ground simultaneously, but asynchronously. Contexts in which this call was given on the ground included: (1) as a response to a chick being handled (2 days); (2) as an observer with a light walked nearby (6 nights); (3) in response to other birds giving Type 2 and Type 3 aerial displays (4 nights); (4) by females in response to male territorial calls given on the ground (3 days); (5) in response to adults giving distress calls (2 days). The contexts in which Type 1 calls are given in the air are unknown.

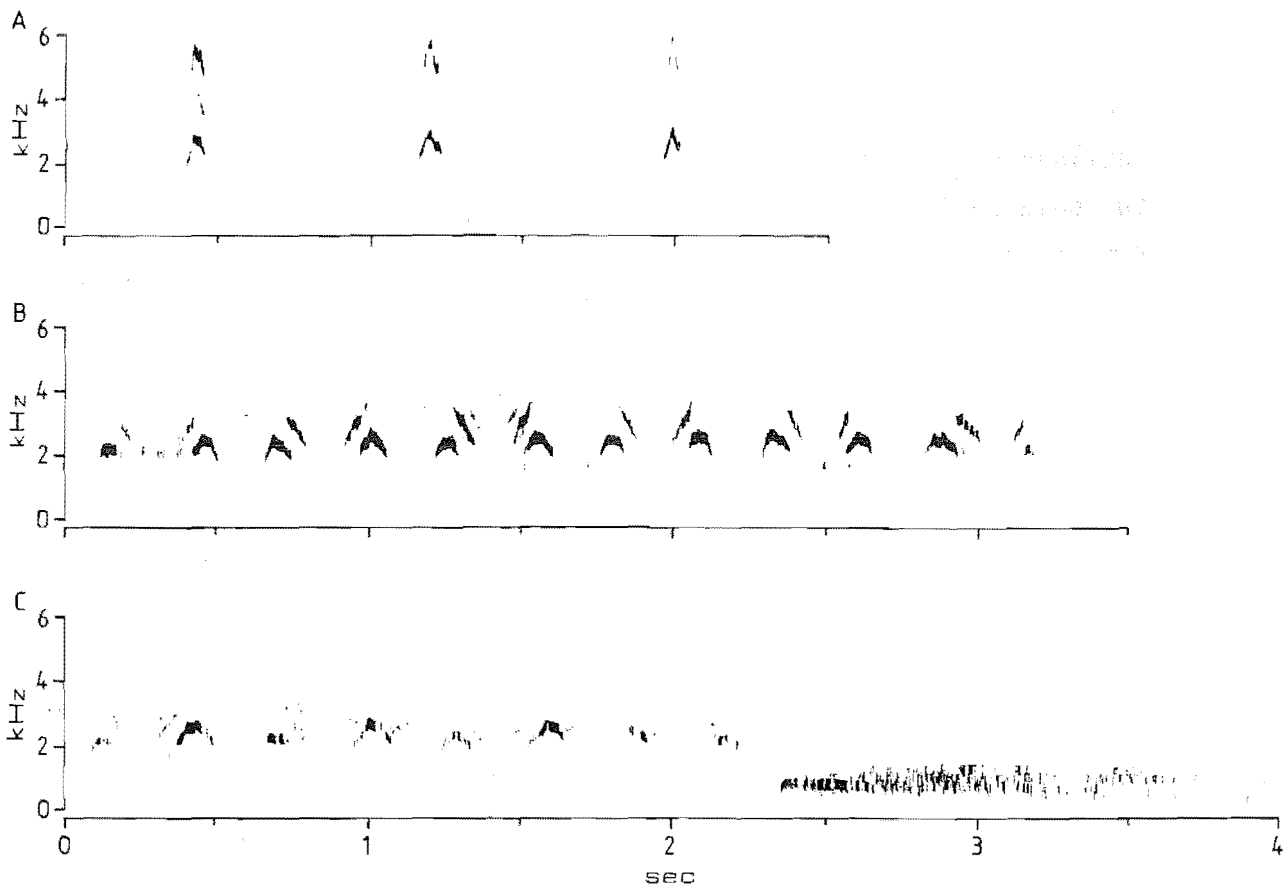

Figure 9.1. Sonagrams of aerial displays of Chatham Island Snipe. A. Type 1. A strident *chep*. Recorded 20:40 11 July 1986, Rangatira Island. B. Type 2. Disyllabic whistle. Recorded 20:30 11 July 1986, Rangatira I. C. Type 3. Disyllabic whistle followed by non-vocal roar. Recorded 23:30 9 January 1984, Rangatira I.

Aerial displaying was not observed for Snares Island Snipe, but they gave Type 1 calls infrequently from the ground (8 days, 7 nights).

Type 2 display (Fig. 9.1b) was a disyllabic *queeyoo queeyoo* given at a rate of approximately 2/sec and repeated four to eight times (n = 21). This call, although given in flight, was identical to a common territorial call given on the ground by male *Coenocorypha* snipes (see sonagrams for Antipodes Island Snipe in Warham & Bell 1979; and for Chatham Island Snipe in Appendix 1). At least five Chatham Island Snipe gave Type 2 calls in the air at night on 11 July 1986, and isolated calls were heard on three nights in 1983-84. Male Snares Island Snipe gave this call every day as a territorial display on the ground, but I never heard it from a flying bird.

The most spectacular aerial display (Type 3: Fig. 9.1c) included a non-vocal component. This display started with the same vocal calls as in Type 2 (usually repeated five times, n = 10), but as soon as these calls ceased there was a loud roar, similar to a distant jet passing overhead and lasting about 1.5 s (n = 3). Type 3 displays were heard on four nights in 1983-84. D.V. Merton (pers. comm.) has heard this display on Rangatira and Mangere Islands (Chatham Is) in every month except April, July, August and September.

Although Chatham Island Snipe is the only form of *Coenocorypha* for which there are tape-recordings of aerial displays, there are written descriptions of Type 3 displays for two subspecies of New Zealand Snipe (ie. Antipodes Island Snipe and the extinct Stewart Island Snipe; Appendix 1).

The non-vocal component of Type 3 aerial displays is thought to be caused by air currents vibrating the rectrices, homologous with the 'drumming' or 'bleating' of *Gallinago* snipes. Unusual tail-feather wear, attributed to aerial displaying, was found on ten *Coenocorypha* snipe skins in New Zealand museums (Appendix 1), including Chatham Island Snipe, Stewart Island Snipe, Antipodes Island Snipe and Auckland Island Snipe. Three live Chatham Island Snipe with worn tail feathers were found among 147 handled on Rangatira Island. The only living form of *Coenocorypha* snipe for which there is no evidence of aerial displaying is the Snares Island Snipe.

Aerial displaying is thought to be performed predominantly by males, as only one known female with worn rectrices has been handled. Excluding Snares Island Snipe, 11 of 88 (12.5%) male *Coenocorypha* snipes handled had worn tail feathers, whereas only one of 97 (1.0%) females did. Displaying probably occurs at any time of year; observations are too few to assess whether the frequency of displaying varies with season.

Flying ability

Coenocorypha snipes are confined to small, isolated islands free of terrestrial predators (Appendix 1). During daylight hours snipe stayed under forest, or among dense tussock grass *Poa* or sedge *Carex*, presumably to avoid diurnal aerial predators. *Coenocorypha* snipes generally only flew during the day if flushed (eg. by people, or crash-landing Sooty Shearwaters *Puffinus griseus*). Other than wing-assisted jumps up or down from logs and banks, I saw only three 'voluntary' daytime flights during 18 months observing *Coenocorypha* snipes. All three were under forest, and were by males (two *C. a. huegeli* and one *C. pusilla*) flying near the ground for 10 - 25 m towards other males calling within the fliers' territories. Most snipe, when disturbed, moved off on foot or avoided detection by 'freezing'. If flushed, *Coenocorypha* snipes usually flew for less than 5 m. Exceptionally, snipe flew 40 m when flushed under open forest with little ground cover. Anderson (1968) claimed flights of "several hundred yards" for *C. a. huegeli*, but how these were determined is not known as except in a few localities the topography and vegetation of the Snares Islands make it impossible to observe such distances.

At night, snipe of both species frequently fed up to 120 m from the nearest cover. Snipe flushed more readily at night, taking off vertically, then allowing the wind to carry them along. Chatham Island Snipe were flushed significantly more often than Snares Island Snipe (35% of 20 nights for *C. pusilla*, 13% of 134 nights for *C. a. huegeli*, $X^2 = 6.6$, $P < 0.01$). Chatham Island Snipe also flew for significantly greater distances (50 ± 14 m, n = 6) than Snares Island Snipe (14 ± 6 m, n = 17, Mann-Whitney $U_s = 102$, $P < 0.001$).

Chatham Island Snipe have flown greater distances. Snipe reintroduced to Mangere Island in 1970 and 1972 subsequently colonised Little Mangere Island - this involved a flight of 300 m across sea, and a vertical rise of about 100 m. Snipe recently sighted on the east and north-east coasts of Pitt Island, Chatham Islands presumably flew from Rangatira Island (2.5 km) and Star Keys (15 km) respectively. Chatham Island Snipe, other than those flushed or performing aerial displays, were seen in flight at night three times. I have never seen Snares Island Snipe in flight at night except when flushed.

Male Chatham Island and Snares Island Snipes had lower wing-loadings than conspecific females. The intersexual difference in wing-loadings was significant for Snares Island Snipe (♂♂ 46.1 ± 2.6 Nm^{-2}, ♀♀ 48.8 ± 4.7 Nm^{-2}, $t_{27} = 2.57$, $P = 0.02$), and approached significance for Chatham Island Snipe (♂♂ 38.2 ± 2.0 Nm^{-2}, ♀♀ 40.4 ± 4.7 Nm^{-2}, $t_{27} = 1.76$, $p = 0.08$). These results support qualitative assessments of intersexual flying ability for both populations: males flushed three times as often as females for both species, and aerial displays of *C. pusilla* were thought (based on tail feather wear) to be performed mainly by males. Chatham Island Snipe had significantly lower wing-loadings than Snares Island Snipe (♂♂ $t_{29} = 10.32$, $P < 0.001$; ♀♀ $t_{25} = 6.86$, $P < 0.001$).

Discussion

Reduction in flying ability of *Coenocorypha* snipes is apparently a recent trait. All living forms are thought to have flown to their remote island homes from mainland New Zealand, probably since the end of the Otiran Glaciation 10,000 years ago (Fleming 1982), yet no form is considered capable of prolonged flight now. The decline in flying ability of *Coenocorypha* snipes was possibly due to a combination of selective pressures against flying. *Coenocorypha* snipes are non-migratory, and as they occur on islands lacking ground-dwelling predators there is little need for escape flights. Little is known about movement of snipe between islands within an archipelago, but these distances are generally small (< 15 km). There are apparent costs associated with flights by *Coenocorypha* snipes, including exposure to aerial predators (eg. Southern Great Skua *Stercorarius skua lonnbergi*, Southern Black-backed Gull *Larus dominicanus*, Red-billed Gull *L. novaehollandiae*, Australasian Harrier *Circus approximans* and New Zealand Falcon *Falco novaeseelandiae*) and the risk of perishing at sea while attempting to move between islands. The poor flying ability of *Coenocorypha* snipes has rendered them vulnerable to recently introduced ground-dwelling predators. Weka *Gallirallus australis*, feral cats *Felis catus* and ship rats *Rattus rattus* have eliminated snipe from at least 11 islands in the last 100 years (Appendices 1 & 3).

Aerial displays by other species of snipe are also given mainly by males, and are thought to be used in mate attraction and territory defence (Tuck 1972, Cramp & Simmons 1983). Snares Island Snipe performed these functions using ground displays. However, the sexual difference in wing-loadings of Snares Island Snipe suggests that either aerial displays have only recently been lost from the display repertoire, or there is some other benefit to males having greater flying ability than females.

Non-vocal acoustic aerial displaying evidently arose before the split between the *Gallinago* and *Coenocorypha* lineages. Aerial displays by the world's snipes have been reviewed by Tuck (1972) and Sutton (1981). Most species have a predominantly non-vocal 'drumming' display that may be punctuated by bouts of vocalisations. However, the three 'Chubbia' snipes (*sensu* Peters 1934) of South America have a predominantly vocal aerial display immediately followed by a non-vocal acoustic display. Cordilleran Snipe *Gallinago stricklandii*, Andean Snipe *G. jamesoni* and Imperial Snipe *G. imperialis* display only at night or during twilight, and have displays qualitatively similar to Type 1 and Type 3 displays of *Coenocorypha* snipes (see descriptions by Reynolds 1935, Vuilleumier 1969, and Terborgh & Weske 1972 respectively). The main display of Cordilleran Snipe and Andean Snipe begins with a loud *cha-woo* (Reynolds 1935) or *whee-tschwu* given at about two calls a second (Vuilleumier 1969) and followed by a 'whir' (Reynolds 1935) or muffled bellow (Vuilleumier 1969).

Structural similarities between the 'Chubbia' and *Coenocorypha* snipes have long been recognised (Hutton 1871, Seebohm 1888, Iredale 1913, Lowe 1915, Meinertzhagen 1926, Kirchner 1972, Tuck 1972, Hayman *et al.* 1986), although the 'Chubbia' snipes are 2 - 3 times larger (Tuck 1972). The similarities in aerial displays reported here supports a common ancestry for these two groups of southern hemisphere snipes.

Appendix 5

Faecal analysis of the diet of New Zealand Snipe on the Snares Islands.

Table 10.1. Soil-dwelling invertebrates identified from remains in faeces of Snares Island Snipe. Numbers for oligochaetes (setae) on the semiquantitative index 0-4 (absent to abundant), other numbers indicate minimum number of individuals present. % = percent occurrence, n = total minimum number of each prey item represented, (ℓ) larvae, (a) = adults, P = present. From Miskelly (1984).

	FAECAL SAMPLES																					
	ADULTS																CHICKS				%	n
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
Oligochaeta																						
gen & sp. 1	2	1	4	3	3	1	2	4	2	3	3	4	2	4	4	4	4	4	3	2	100	-
gen & sp. 2					1			3			2	1		3	3	2	2			2	45	-
Amphipoda	3	1	2	1	3	1		3	1	1	3	5	1	1	5	1	1	1	1	2	95	37
(*Parorchestia* sp.)					P																	
(*Makawe parva*)								P			P				P							
(*Transorchestia bollonsi*)																				P		
(*Talorchestia patersoni*)															P							
Opiliones																						
Laniatores																						
Hendea sp.								1													5	1
Aranea																						
Agelenidae																						
Myro sp.											1		1			1					15	3
Acari				1		1				1	1					2				1	30	7
Orthoptera																						
Stenopelmatidae																						
Zealandosandrus subantarcticus											1										5	1
Coleoptera																						
Carabidae																						
Mecodema alternans (ℓ)											1										5	1
Diglymma castigatum (a)	1		1	1	2			1	1	1		1				1					45	10
Synteratus ovalus (a)			1																		5	1
Leiodidae																						
Paracatops sp. (a)	1			1		1							1	1							25	5
Staphylinidae (ℓ & a)	1										1		1			1				2	25	6
Scarabaeidae																						
Prodontria longitarsus (ℓ)											6						1				10	7
" " (a)	2		1		1		1	1			1		1		1						40	9
Byrrhidae																						
Epichorius tumidellus (a)											1										5	
Synorthus insularis (ℓ)			1			2						2	1			1	1				30	8
" " (a)	1				1																10	2
Anthribidae																						
Cacephatus aucklandicus (a)						1									1						10	2
Curculionidae																						
Notacalles planidorsus (a)											1									1	10	2
Phrynixus laqueorum (a)						1															5	1
Gromilus laqueorum (a)			1	1	1	1				1	2	1	1	1							45	10
Nestrius laqueorum (a)	1	1			1			1													20	4
Diptera																						
Tipulidae																						
Leptotarsus sp. (ℓ)									3												5	3
% vegetation	25	20	10	-	P	P	5	25	5	-	5	P	-	P	-	-	5	P	-	-	65	-